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THE MIGRATION AND CONSERVATION OF SALMON

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Edited by

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FOREWORD

This is the first symposium in the field of the biological sciences to be published for the American Association for the Advancement of Science. But there have been several in the related field of medicine and public health—*The Cancer Problem, Tuberculosis and Leprosy, Syphilis,* and *Mental Health*—and two in the field of chemistry—*Applications of Surface Chemistry in Biology* and *Recent Advances in Chemical Physics.* The symposia that have been published are, however, only a fraction of the broad surveys and integrations of science, often ranging far across the boundaries that separate its usual divisions, which have been organized and presented at the meetings of the Association.

Plans for this symposium on *The Migration and Conservation of Salmon,* like those for each of the earlier symposia, were developed by distinguished specialists. All the participants in the symposium were invited and their contributions together constitute a comprehensive, integrated and annotated digest of what is known about an important and interesting subject. Since salmon are found in the waters of the United States, Canada and Great Britain, one or more specialists from each of these countries contributed to the symposium.

On the day following the presentation of the symposium, the participants in it and others met in two half-day sessions for free and informal discussions and criticisms of the formal papers. Fortunately these informal discussions were reported stenographically, for they proved to be so valuable that, as edited by Dr. A. G. Huntsman, they are included in this volume.

In the problem of accounting for the migration of salmon one enters a field in which science and romance appear to meet. At least it has often been maintained that the mature fish, moved by some strange super-human instinct, return after several years at sea to precisely the stream of their birth and there, in their first home, deposit and fertilize their eggs, to begin a new generation. The method of science, however, is to look for explanations of phenomena in the general properties of the world about us, even though at first this seems to us almost or quite supernatural. During the past two or three decades these methods have been extensively used in attempts to account for the migrations of salmon. Not only have the currents and the temperatures and the chemical constitutions of the waters in which they live been extensively surveyed, but salmon of various ages in numbers running into tens of thousands have been tagged and hundreds of thousands have been marked. In spite of the fact that large numbers of these tagged or marked salmon have been recovered, as reported in detail in this symposium, the story of what takes place in their migrations is yet far from being complete, and the explanations of them are as much open to question. It is for these very reasons that this volume is timely and valuable from the scientific point of view. And it will likewise be of interest not only to those who fish and hunt because of the spirit of the chase that still lives in us, but also to the countless numbers who feel a dim and ill-defined kinship with all living things on the earth.

F. R. Moulton

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TABLE OF CONTENTS

I. INTRODUCTION. A. G. HUNTSMAN 9

II. ATLANTIC SALMON. 13

1. Some Preliminary Observations on the Migrations of the European Salmon. W. J. M. MENZIES 13

2. The Atlantic Salmon of the Gulf of St. Lawrence. DAVID L. BELDING 26

Salmon Cycles 27

Salmon Characteristics 27

Seasonal Runs of Salmon 28

Tagging Experiments 29

Summary 31

3. Migration and Conservation of Atlantic Salmon for Canada's Maritime Provinces. A. G. HUNTSMAN 32

The St. John Salmon 33

The Miramichi Salmon 34

Relation of Salmon to River Influence 36

Passive Transportation 36

Active Movements 39

More Rapid Movement to Distant Places 41

Movements in the River 42

Conservation 43

Summary 44

III. PACIFIC SALMON. 45

1. Local Populations and Migration in Relation to the Conservation of Pacific Salmon in the Western States and Alaska. WILLIS H. RICH 45

Summary 49

2. The Migration of Pacific Salmon in British Columbia Waters. W. A. CLEMENS, R. E. FOERSTER and A. L. PRITCHARD 51

Methods 51

The Migration of Spring Salmon 51

The Migration of Sockeye Salmon 54

Marking of Pink Salmon 55

Marking of Sockeye Salmon 56

Discussion 57

Importance of Knowledge of Migration to Conservation 58

Summary 58

3. Factors Controlling Salmon Migration. HENRY B. WARD 60

The Parent Stream Theory 60

Scale Markings 63

Return of Planted Fish to Salmon Streams 64

Plantings of Salmon in Foreign Waters 65

Experiments in Marking Young 66

Wandering Fish 68

Tagging Adult Salmon in Salt Water 69

Evidence of Environmental Control 70

Summary 70

4. Chemical Factors Affecting the Migratory Movements of the Pacific Salmon. EDWIN B. POWERS 72

Summary 83

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IV. CONFERENCE ON SALMON PROBLEMS.

David L. Belding, J. J. Cowie, A. G. Huntsman, W. J. M. Menzies, G. Prefontaine, Edwin B. Powers, Willis P. Rich, J. A. Rodd, Henry B. Ward 86

Separate Biological Races 86

Sea Habitat of Salmon 88

Behavior of Salmon in the Sea 92

Behavior of Salmon in the River 94

Post-smolts and Condition Factor 99

Distribution of Spawned Salmon or Kelts 100

Factors Affecting the Movement of Salmon 100

Temperature 100

Sexual Maturity 101

Light 101

Turbulent Currents 102

Random Movements vs. Directed Movement 102

Odors 103

Conservation 104

Summary 106

INTRODUCTION

Since salmon angling causes its devotees to migrate from country to country for the thrill it affords, the clubs on the salmon rivers of northern New Brunswick and Quebec are decidedly international in character. It is not surprising, therefore, that on becoming alarmed over decreases in the stocks of salmon in these rivers, they brought to their assistance Dr. D. L. Belding, of Boston, who had been prominent in fisheries investigation in Massachusetts, Mr. W. L. Calderwood, of Edinburgh, with a life-time of experience with Atlantic salmon, latterly as Inspector of Salmon Fisheries of Scotland, and Dr. Henry B. Ward, of Illinois, noted for his studies on the behavior of the Pacific salmons. These clubs shared a rather general belief that the salmon of their rivers migrate to and from the open Atlantic ocean through the Gulf of St. Lawrence and past the Maritime provinces and Newfoundland, where they would be liable to capture.

Failure of scientific agreement on this matter at a conference with Canadian Government officials at Ottawa on February 7 and 8, 1936, not only stimulated investigation as well as discussion of the subject in scientific journals, but also led to the proposal by Dr. Ward that the migration and conservation of salmon in general form the subject of a symposium for the meeting of the Association at Ottawa in June of 1938.

All the invitations to participate in the symposium were accepted and it was held in the Chateau Laurier, Ottawa, on the morning of June 29, 1938, although Drs. Clemens, Foerster and Pritchard, of British Columbia, were unable to be present in person. As the time allotted did not permit opportunity for discussion, the participants were invited to meet the following day in the office of Mr. J. J. Cowie, Secretary of the Fisheries Research Board of Canada. At this meeting, which lasted the entire day, there was very free discussion of the controversial matters dealt with in the symposium. It was decided to include the more significant parts of this discussion in the published account.

Apart from its connection with the practical problem of getting sufficient salmon for food and for sport, the migration of these fish is of very great scientific as well as general interest. Mass movements of animals are often of such a striking character as to stimulate enquiry concerning the forces behind them. In this as for nearly any kind of animal behavior, scientists tend to divide into two schools—those who expect the "*nature*" of the animal to afford the explanation, and those who look for it in "*nurture*" or environment. Actually, of course, both the animal and its environment are always involved, and the problem is to determine the extent of the role played by each. Disputed scientific points can best be settled by precise experiments, but migrations in the ocean and in the rivers scarcely lend themselves to precise experimentation. If at the same time the matter is very complex, as seems probable, the problem will not be readily solved.

The migration of salmon may well be taken to typify the migration of fish in general as is seen by the prominent position it has occupied in books on fish migration. It is a very striking migration—from breeding grounds in rivers, perhaps many miles up most turbulent and swift streams, to more or less unknown places in the sea, where the main growth takes place. Where are these places? What are the salmon's movements thither and thence, and how are these determined? To what extent do the salmon return and spawn in the streams where they are born? Such questions have been in the minds of the investigators, who with diverse backgrounds of experience have dealt, each in his own way, with the migration of salmon in this symposium.

The Salmon family (Salmonidae), as occurring naturally, are confined to the coasts, rivers and lakes of the Arctic and North Temperate zones, which has long been known, the most recent critical considera-

tion of the family as a whole (C. Tate Regan, Ann. Mag. Nat. Hist., *13,* p. 405, 1914) giving no extension of this range. They breed in fresh water streams or lakes and may or may not migrate to the sea, even in the one species.

The family is typified by the genus *Salmo* and the species *S. salar,* the Atlantic salmon. It includes a larger or smaller number of genera depending upon the classification adopted. American ichthyologists place the whitefishes and the graylings in separate families, the Coregonidae and the Thymallidae. Similarly for the arrangement of the species in genera, the American ichthyologists, following the classical works of Dr. David Starr Jordan and his collaborators, place the Great Lake trout, a former member of the genus *Salvelinus,* in a separate genus *Cristivomer,* and separate the Pacific salmons from *Salmo* to form the genus *Oncorhynchus.* There are also the North Asian genera, *Hucho, Brachymystax, Phylogephyra,* and *Stenodus,* the last alone ranging into North America in its very northwestern part. Apart from the extent of the subdivision into genera, there are divergent views as to the relationships of particular species. Some of those occurring in western North America, *e.g.,* the Rainbow trout or Steelhead salmon, are placed in the genus *Salmo* by American ichthyologists, but are considered by Regan as more nearly related to the species included in the genus *Oncorhynchus* than to the Atlantic salmon.

It is not perhaps surprising that the common names of these fishes should be in a somewhat confused state. The term "char," used in Great Britain for species of the genus *Salvelinus,* has little vogue in North America, where "trout" is the usual name, and even "salmon" is used. Some species of the genus *Salmo* are called, not "salmon" but "trout," both in North America and in Great Britain. The term "salmon" used in the title of this symposium, does not correspond with any taxonomic group. From the scientific standpoint, it is somewhat unfortunate that this name, given originally to the Atlantic salmon, has been extended to include five species of Pacific fishes, those in the genus *Oncorhynchus,* which, unlike the Atlantic salmon, die after first spawning, a peculiarity of very general interest. The behavior of migrating between fresh and salt water is, however, fairly general through the family and not in correspondence with any classification.

The Atlantic salmon (*Salmo salar*) occurs on both sides of the Atlantic and is the typical and best known member of the family. The individuals of this species characteristically migrate to and from the sea, although some, thought to constitute a subspecies or variety, fail to leave the lakes in which they occur.

In this symposium, three out of the five species of salmon on the Pacific coast of North America have been considered, as well as the Atlantic salmon. The principal one of these is *Oncorhynchus nerka,* variously known as the red, sockeye or blueback salmon. Some individuals of this species are non-migratory, not leaving the lakes in, or above, which they spawn and never becoming large. W. E. Ricker (J. Fish. Res. Board Can. *4,* p. 192, 1938) has recently distinguished among these individuals those which seem to form a separate sub-species (*O. n. kennerlyi*), known as the kokanee, and those for which he proposes the name "residual" sockeye "because the evidence shows that they are, at least in large part, the progeny of anadromous parents," that is parents that have been to sea. The other two species are *Oncorhynchus tschawytscha,* the chinook, spring or quinnat salmon, and *Oncorhynchus gorbuscha,* the pink or humpback salmon. The former spawns in the upper waters of large streams, sometimes as much as a thousand miles from the sea, grows to a large size, and may travel very long distances in the ocean. The latter does not go far upstream to spawn, and matures at the end of its second year, being then only from three to six pounds in weight. It should be noted that the Pacific salmon die after the first spawning, while the Atlantic species may spawn as many as five times.

The various stages in the life history of these fishes have been given distinct names, which were first applied to the Atlantic salmon. For a long time some of these were thought to be distinct species rather than stages in the life of one species. Those given and defined below are for the Atlantic salmon, and are not necessarily applicable to other species.

The eggs hatch while the yolk is still in large amount, and the young fish with its large yolk sac is known as an *"alevin."* Not until the yolk is practically all used up does the fish emerge from the gravel bed in which the eggs were laid. It soon develops a color pattern, whose most pronounced feature is a series of vertical bars along each side, and this stage is called a *"parr."* When about to descend seaward, the parr begins a transformation, which results in the bars becoming obscured by the development of a silvery coat of guanin crystals. The fish at this time is rather similar in size and appearance to a smelt and is known as a *"smolt."*

In the sea the smolt grow very rapidly and within a year or two weigh about five pounds. They are then called *"grilse."* When, after another year, their weight has increased to about ten pounds, they are merely called salmon. Irrespective of size, those that have not spawned are known as *"virgin"* or *"maiden"* salmon; and those that have spawned, while still thin, are known as *"kelts,"* but after feeding and becoming plump again are known as *"clean"* salmon.

A. G. HUNTSMAN

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SOME PRELIMINARY OBSERVATIONS ON THE MIGRATIONS OF THE EUROPEAN SALMON

By W. J. M. MENZIES

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WITH a view to tracing the migrations of salmon in European waters the fish have been marked at three stages in their lives, viz., as smolts, clean fish and kelts. Smolts and kelts have been dealt with when descending to the sea and clean salmon chiefly in salt water. Such operations were started in Scotland about 40 years ago, and since then have been extended to Norway, Ireland, England and practically all of the countries bordering on the Baltic.

Smolt marking has produced no evidence of the movements of the salmon in the sea, either when feeding or returning to fresh water, except in the Baltic. It will perhaps be most convenient to deal now with these last results and with the other aspects of the life of the fish in that sea, since they form a self-contained community divided from the salmon of the Atlantic by a line drawn from Denmark to Sweden across the narrow western neck of the Baltic. Investigations have been made chiefly by Dr. Gunnar Alm of Sweden and these, together with the work of his countryman Dr. Nils Rosen, of Professor Jarvi in Finland and others, he has summarized in a publication of the International Council for the Exploration of the Sea (Alm, 1934).

The results achieved in this small sea are of particular interest as showing the consistent yet somewhat complicated movements of the salmon from their native rivers to their feeding grounds and then back again to the rivers. Put quite shortly, the marking of smolts and adult fish and the reading of their scales show that the smolts from the rivers on the west side of Finland, and from the north and middle of Sweden proceed down the Swedish coast to the southwestern corner of the Baltic (Fig. 1). From the north Finland rivers the smolts proceed down the other side of the Baltic, across the mouth of the gulf of Bothnia and down to the Polish and Pomeranian coast. This migration on the eastern side of the Baltic is of special interest since these northern fish pass the smolts and young salmon originating from the rivers of Esthonia and Latvia. The explanation seems to be that the latter fish find an adequate quantity of the food comparatively close to their native rivers, but that a more far reaching migration, equivalent to the migration carried out by the salmon of the west Finnish rivers, takes the northern Finnish salmon on past these feeding grounds to yet better areas further south. In their early stages the little fish feed on *Gammarus sp.* and later on *Ammodytes sp.* and no doubt small herring also.

The exact distribution of the small and feeding fish in the southern part of the Baltic depends upon the prevailing wind and the spread of the food supply. The smolts of the current year arrive at the south of the Baltic in the autumn months and thus take approximately three to five months for a journey of up to eight hundred miles. At first in general the Swedish smolts are found in the southwestern corner but later they may move out round Bornholm and towards the Danish, German and Polish coasts where an intensive fishing with both lines and nets is carried out for them in the late winter and spring months. The majority of the catch are "mielnice," as they are locally called, or in other words young salmon in the pregrilse stage. They are from 40 to 50 cm in length and weigh from about 1½ to 2 lb. After April or May they are lost even in this small sea. No doubt some journey northwards and return to the rivers as grilse, but many others remain somewhere in the south-

FIG. 1. MIGRATIONS OF MARKED SALMON IN THE BALTIC (AFTER GUNNAR ALM). Continuous line (———), those marked as smolts; interrupted line (– – – –), those marked as adolescent or adult salmon.

ern Baltic and are again found on the same feeding grounds as two-winter salmon in the following autumn and winter.

The salmon from the rivers of southern Sweden and the opposite side of the Baltic have no need to make migrations of any considerable extent and move out only the requisite short distance to the same grounds as the salmon from the north. In these southern rivers the average smolt age is low (80 per cent two years old). It gradually rises in the more northerly rivers until in the north of Sweden it is high (75 per cent three years old). Yet in confirmation of the marking results, the average smolt age of the young salmon caught in the southern Baltic is high (up to 70 per cent three years old) and is built up by the very old Finnish as well as northern Swedish fish.

In Scotland clean salmon were first marked in the sea in 1913 (Calderwood, 1913, etc.), and in Norway Professor Dahl took up similar work in 1935 (Dahl, 1935, etc.). For many years before these dates a very considerable number of kelts had been marked in the rivers of both countries, but the isolated recapture of some of these, when again clean, in the sea has given only fragmentary information regarding the migrations of the fish in salt water, and I do not, therefore, at present intend to deal *in extenso* with them.

The Scottish sea marking experiments were started in the Moray Firth (Fig. 2) on the northeast side of the country, were continued on the north coast, and during the last two years, as well as in the present year, they have been continued on the west coast. Professor Dahl commenced the Norwegian experiments at stations outside (but on the coast of) the island belt near Bergen. He has also operated a station inside the island belt at the mouth of the Trondheim Fjord and another station in the extreme northwest corner of Arctic Norway on the island of Soroy in West Finmark.

In the course of the later Scottish and the Norwegian experiments there has been a certain interchange of marked fish, and, for a proper understanding of the results, it seems to me that it will be better if they are considered as complementary and not as separate entities. I propose, therefore, to deal with the Scottish work from west to east and

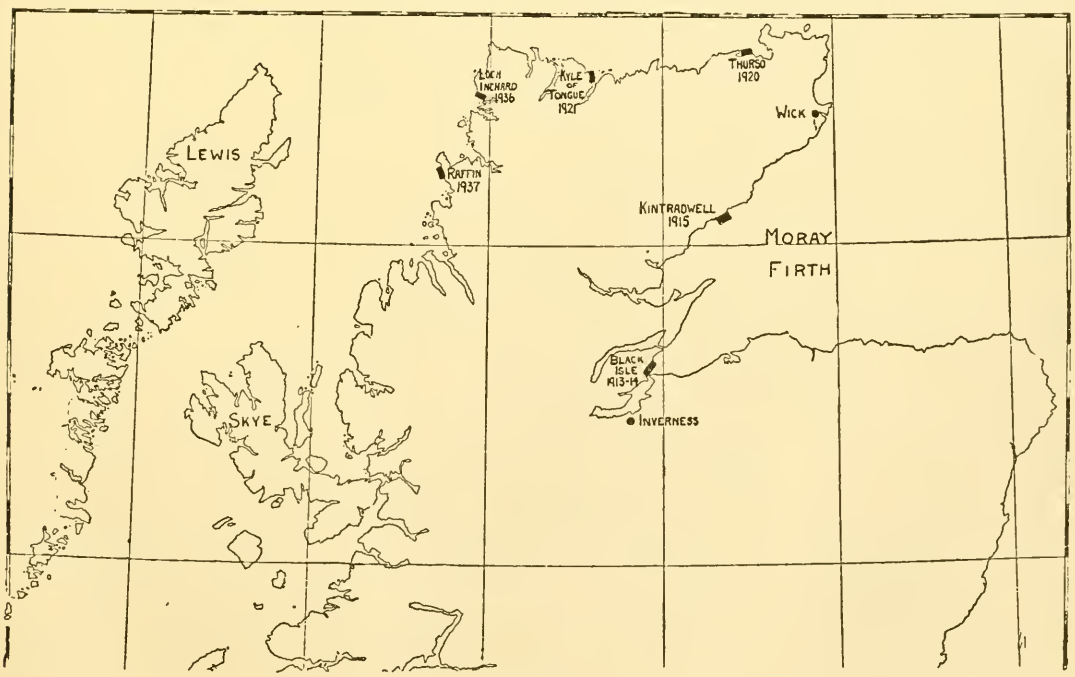

FIG. 2.

not in the chronological order in which it was carried out.

The Scottish station in 1936 (Menzies, 1937) was situated about twenty miles to the south of Cape Wrath at the northwest corner of the country (Fig. 3). From here the marked salmon moved chiefly northwards to Cape Wrath and then eastwards along the north coast; some continued southwards down the east coast. One salmon crossed the North Sea and was recaptured close to Professor Dahl's station in the Sognefjord. For every three fish which started their journey in an easterly direction

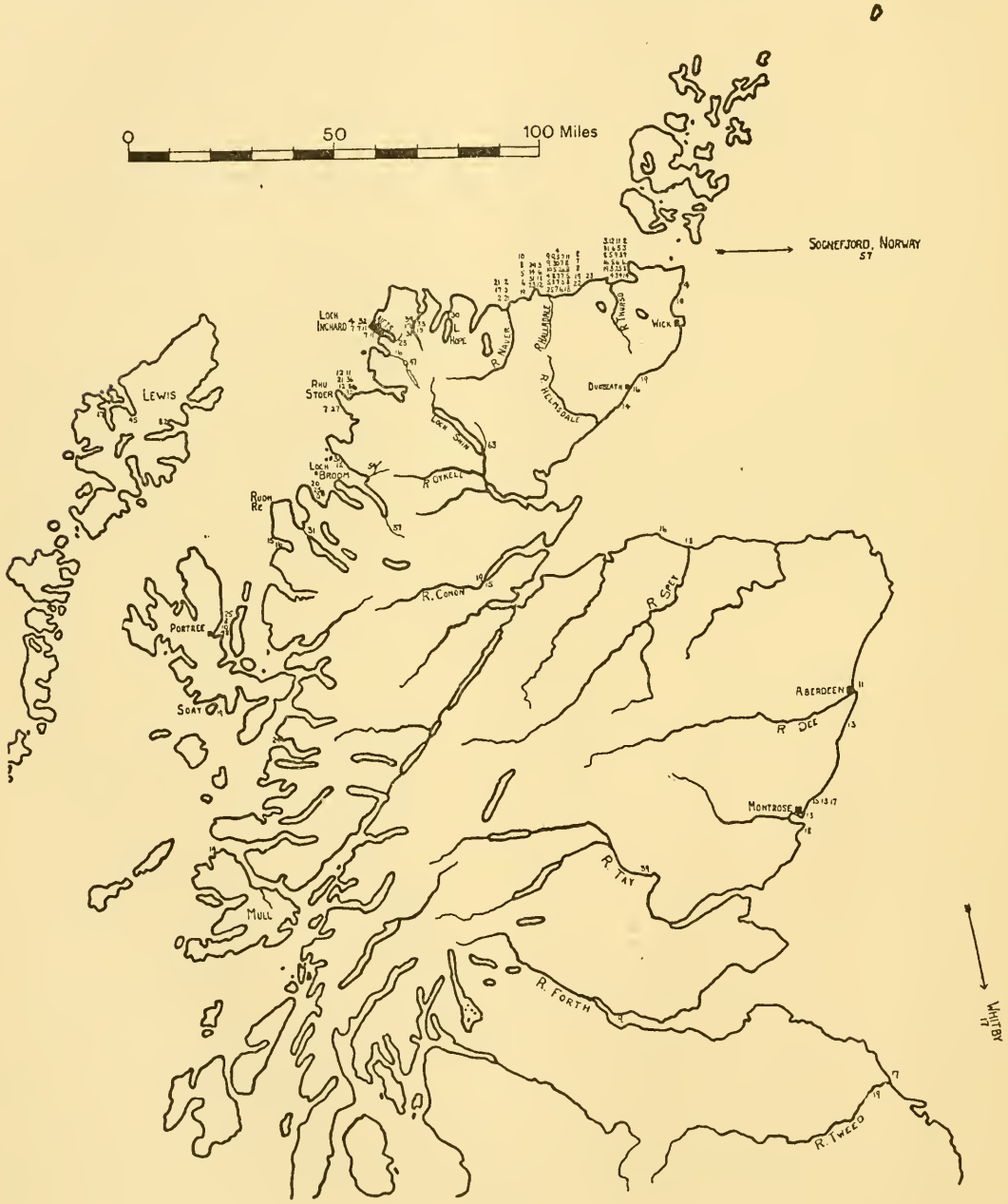

FIG. 3.

along the north coast only one remained on the west coast. Of these latter fish about half were caught within 50 miles of the place of marking and seemed to be destined for rivers in that neighborhood. The remainder went further south to the coast of Skye and two beyond that to Loch Nevis and the island of Mull respectively. Two moved to rivers on the west side of Lewis in the outer Hebrides. As will be seen from Fig. 3, 79 of the 105 recaptured salmon which left the west coast were retaken on the north coast, and the remaining 26 were found on the east coast as far south as the Yorkshire shore beyond the Scottish border.

This general move from west to east was confirmed in 1937, when the experimental station was moved 20 miles further south-

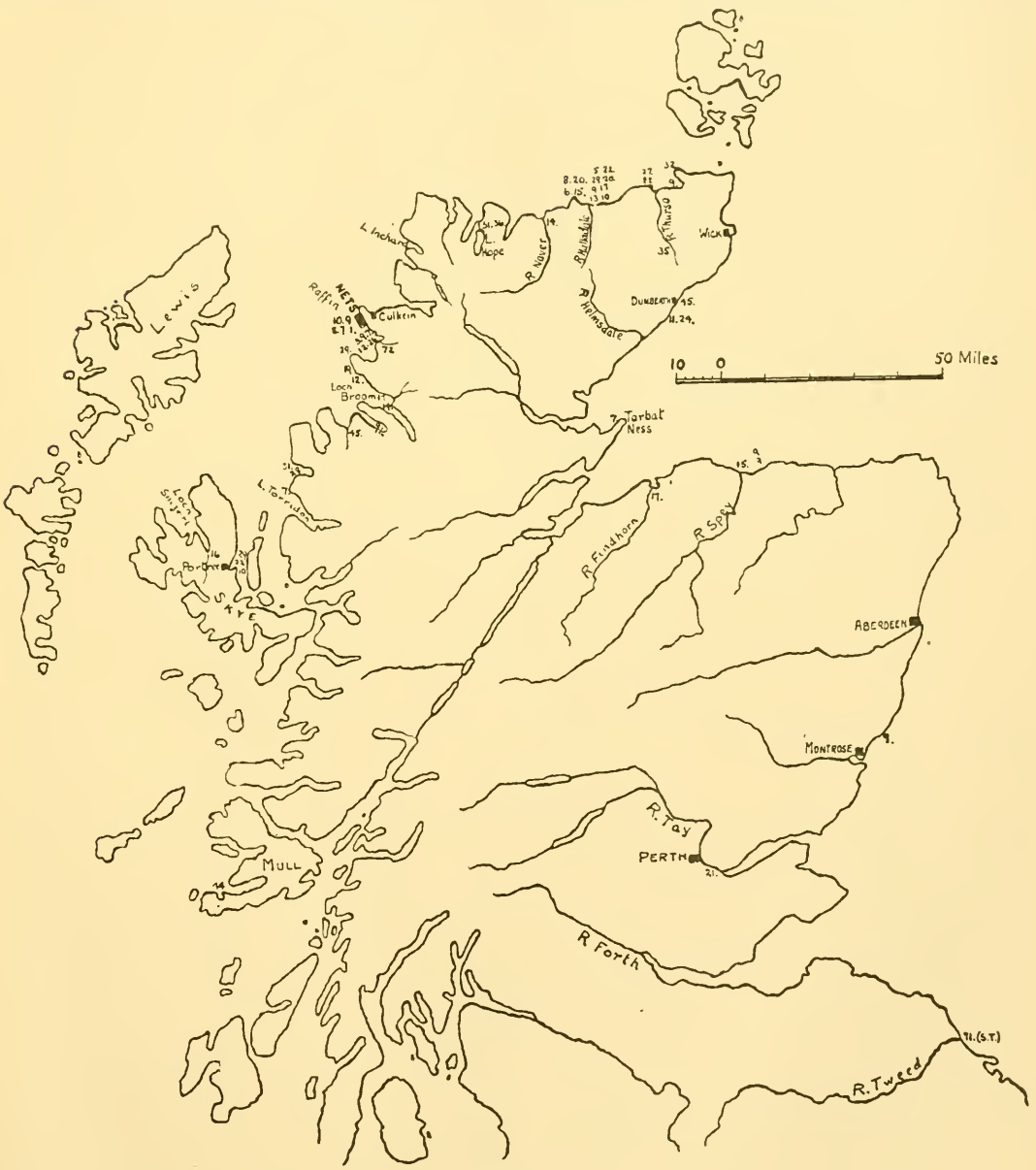

FIG. 4.

wards down the west coast (Fig. 4). From here the majority of the 58 recaptures were again made on the north and east coasts of Scotland but no marked fish were found in Norway and a rather higher proportion (three north and east for every two west and south) remained on the west coast.

The distribution of the salmon arriving at this northwesterly part of Scotland was confirmed by another experiment carried out in 1921 on the north coast about 20 miles to the east of Cape Wrath (Fig. 5). Here very few fish were marked, and of these only nine were recaptured but the nine were distributed as to three on the north coast, four on the west coast and two on the east coast.

The Scottish experiments, which I have indicated in such a brief manner, seem to show that on the northwest and at the west end of the north coast the indications are that a predominant movement of the salmon from the west exists, and I may here add that this indication is confirmed by an experiment which has been started this year further south (at the island of Soay to the south of Skye) on the west coast. All the recaptures (16) of this latter marking reported up to mid-June have been on the north or east coast with the exception of one fish which was retaken within 20 miles of Soay.

If we now turn to Professor Dahl's results (Fig. 6) we find a somewhat striking confirmation of this movement from the west. The first stations in 1935 were outside the island belt at Rong and Titran about two-thirds down the western coast of Norway. From these stations the marked fish distributed themselves both to the north and south of the place of marking. The largest numbers were caught in nets and rivers comparatively close to the marking station, but others were found much further away, some as far south as the Swedish coast, others northwards along the Norwegian coast, one near the North Cape and one in the White Sea; one salmon left the main lines of migration north and south of the place of marking and crossed in a southwesterly direction to Scotland. In 1936 work was continued at these two stations and at another at Maelver between the two older stations. The results confirm those obtained in the previous year and, in fact, are very similar except that no fish went round the North Cape and two, one from the northern and one from the central

FIG. 5.

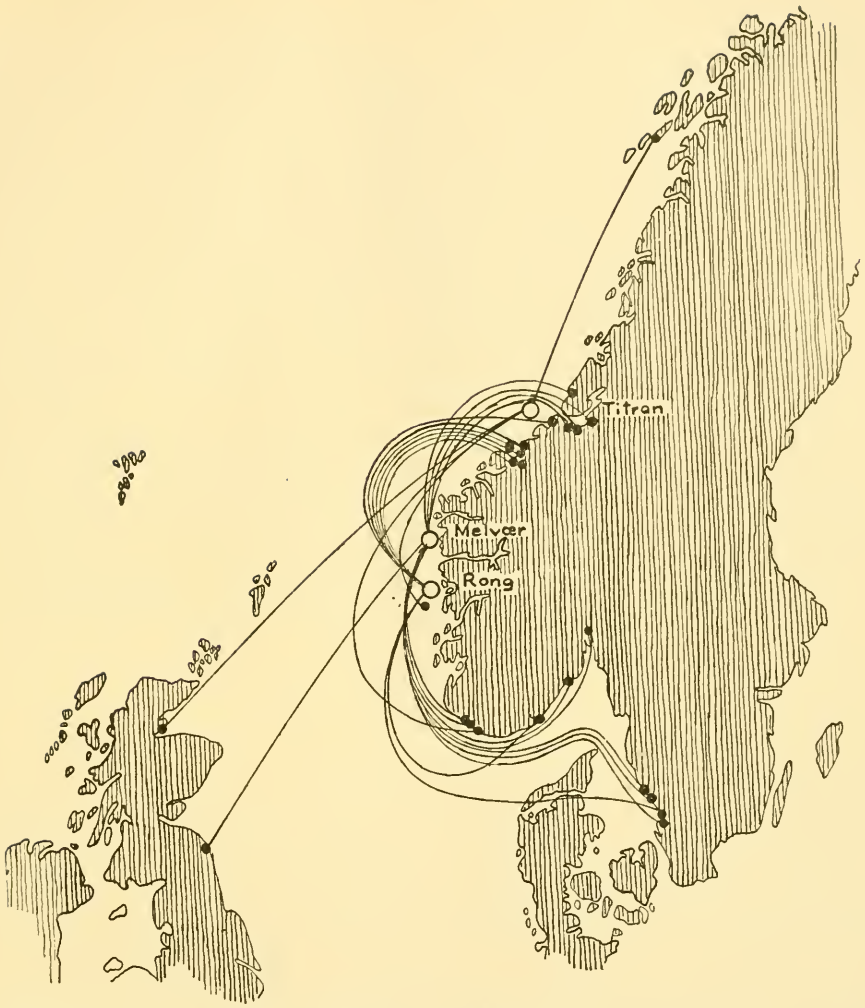

FIG. 6. DISTANT (400 KM OR MORE) MIGRATIONS OF SALMON MARKED IN NORWAY IN 1936. (FROM DAHL AND SØMME.)

station, went to Scotland. Once again the situation was confirmed in 1937 (Fig. 7) (the southern station was not in use); no fish went to Russia but five went from the middle station to Great Britain. In this year (1937) Professor Dahl started another station, a long distance from his earlier stations, on the island of Soroy, West Finmark, and not a great distance from the extreme north of Norway. From this station the results are rather different from those obtained further south. A certain number of recaptures were made within a moderate distance (38 within about 130 miles) and many of these were in the local rivers. Beyond this distance none were captured to the south but in the opposite direction no less than about 90 were taken at a greater distance. These latter were spread along the north coast of Norway, of Finland and Russia to the rivers of the White Sea and beyond even that to the river Petchora, which is reputed to be the eastern limit of *Salmo salar*.

Such is the evidence obtained in Scotland and in Norway of the main migrations of the salmon returning from their feeding grounds. The whole would be consistent with a general move in from the westward towards the coast, and seems to imply a defi-

FIG. 7. DISTANT (400 KM OR MORE) MIGRATIONS OF SALMON MARKED IN NORWAY IN 1937. (FROM DAHL AND SØMME.)

nitely directed journey. The marking stations have been selected only for reasons of convenience, and in my opinion the results must be interpreted not as simple movements from these stations alone, but as indices of what is happening on probably the greater part of the coasts along which the stations are situated.

From the results the inference may be drawn that while the salmon makes a definite migration towards the coast which it is seeking, it does not necessarily set a very accurate course for a definite river and the landfall which it makes may be a long distance from its ultimate destination. In Scotland in 1936 and 1937, 34 salmon made journeys of more than 100 miles between the place of marking and the place of recapture which, in the case of those caught again in coastal nets, was not necessarily close to their final destination had they been allowed to continue their passage. Two of these journeys extended to 400 miles. In 1938 the average length of journey has been increased. Fifteen of the 16 fish reported as recaptured prior to the middle of June had all covered distances of from 200 to 400 miles.

These Scottish journeys have been greatly exceeded by those of some of the fish with which Professor Dahl has been dealing. As in Scotland, he has found the majority of his recaptures within 100 or 150 miles of the places of marking. But in 1937 alone he had no less than 94 salmon which travelled over 150 miles, and of these 17 covered 600 or more miles, one of them journeyed no less than 1,150 miles. In 1935 the salmon which was recaught in the White Sea had covered some 1,600 miles.

That the Baltic salmon should be known definitely to cover up to 800 miles between their native river and their sea feeding grounds, and that the Atlantic salmon should also be known to cover up to say 1,500 miles after it has finished feeding, and has again struck the coast on its way back to fresh water, would seem to dispose effectively of any difficulties which we might have in postulating possible feeding grounds for these latter fish as situated up to say 1,500 miles from both the coast in general

and the particular river from which the fish emerge.

Great difficulty exists when one attempts to estimate the speed at which salmon swim in the sea. A direct comparison of minimum length of journey and the time interval between marking and recapture can give only the slowest possible average speed. We can not know the exact course followed by the fish; nor can we estimate the time which may be spent after marking before the journey is started or before final capture after completion of the main passage. Results do suggest, however, that when the fish is engaged in a long journey it makes the passage in more direct fashion than when a shorter trip is in prospect. The average speeds obtained for the longer trips are almost always higher than those for journeys of only a few miles, and the error introduced by calculations based on days absence is also smaller for the longer time intervals. For instance, a fish marked one morning and recaptured the following afternoon would be counted as absent one day, whereas it has taken one and a half days for the journey—an addition of 50 per cent to the nominal time. Whereas if the total time be say 12 days the error of a half day becomes of much less importance. On the Scottish coast salmon may accomplish journeys greater than 100 miles at an apparent speed of between 20 and 35 miles per day; the latter rate occurs only in the case of two fish both of which travelled more than 250 miles. In general, Professor Dahl has found the same rates of speed although he has a greater number at the maximum rates. He

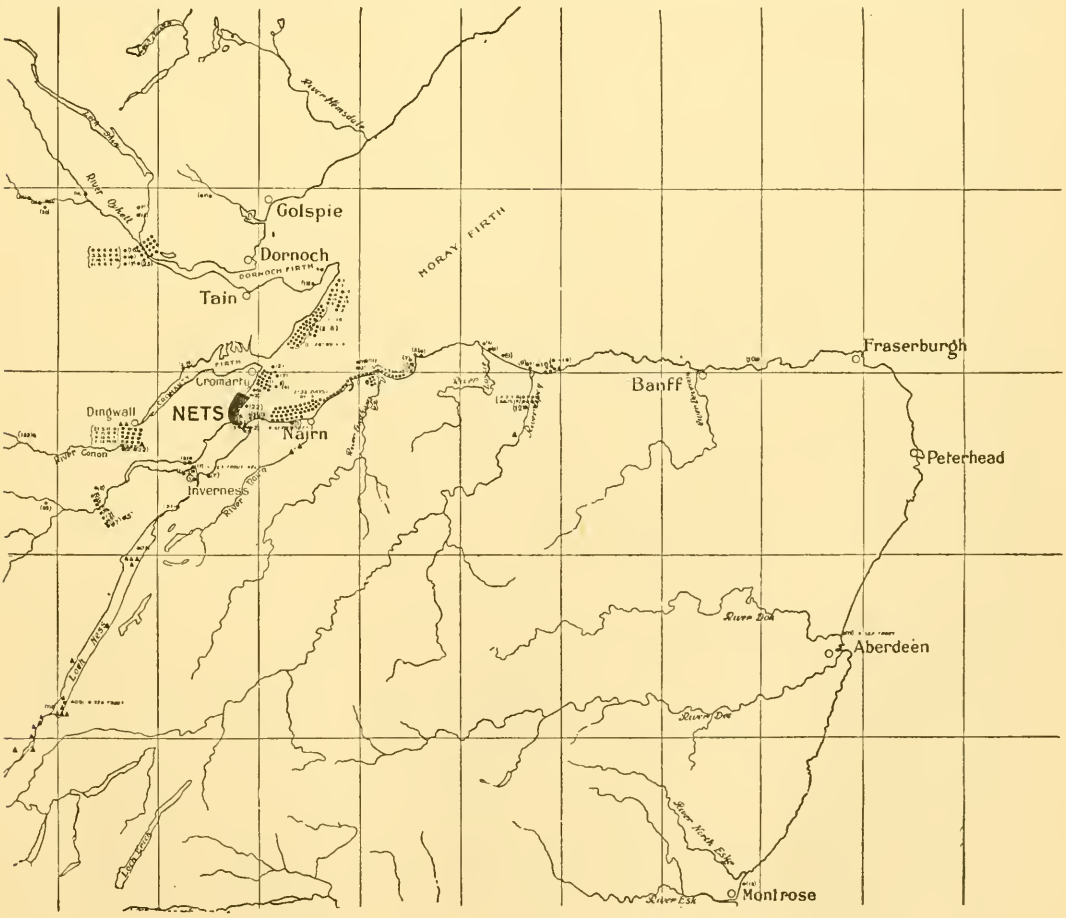

FIG. 8

also has a few fish that travelled up to 45 miles per day and one remarkable specimen which, on the data given, moved at no less than 60 miles per day, over a distance of nearly 700 miles.

In Scotland other marking experiments have been carried out in earlier years which demonstrated among the fish concerned a more local movement than has been shown in the work which I have just mentioned. The results of these earlier experiments were confirmed by the Norwegian fish which were recaptured close to the place of marking and by another station which was established at the mouth of the Trondheim Fjord in that country.

The first sea marking experiments were carried out in 1913 and 1914 in the inner part of the Moray Firth where the distribution of recaptured fish was entirely different from that already described for the north-west coasts and Norway.

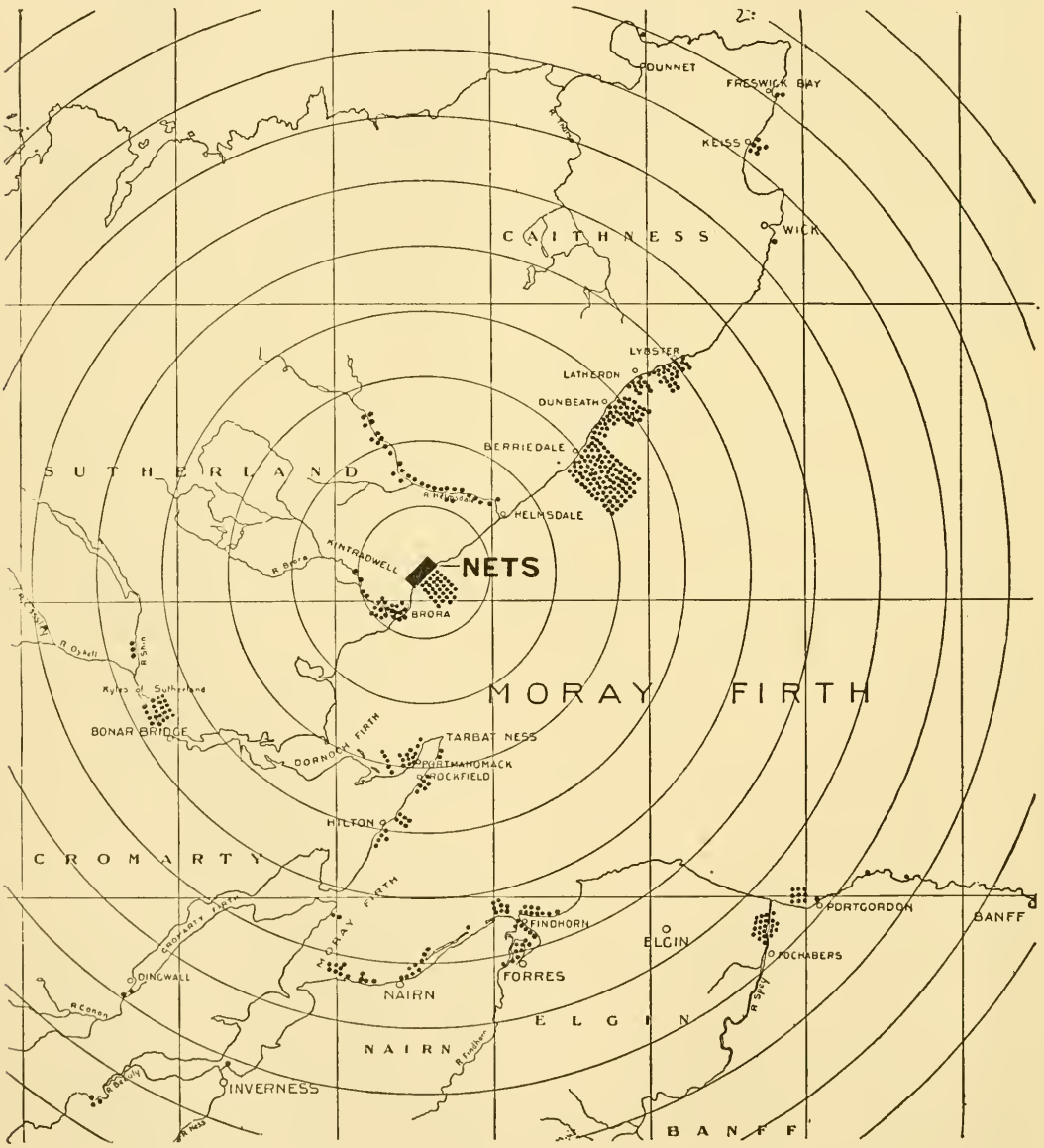

FIG. 9.

The fish marked in the Moray Firth (Fig. 8), with very few exceptions, were not great travellers; they had apparently completed the major part of their journey and were endeavoring to ascend one or other of the local rivers. Practically all were found again within 50 miles of the place of marking and the great majority within 30 miles. The exceptions amounted to only four out of a total of 256 recaptures and the maximum distance was southwards to the Firth of Forth (250 miles). The stock dealt with may therefore be considered to belong to one or other of the 13 rivers which flow into salt water within 50 miles, and most of them at a considerably shorter distance from the place of marking.

In another experiment (Fig. 9) further to the north on the east coast of Sutherland, but still in the Moray Firth, the same result was brought out. Here a radius of 40 miles covers all but a very small percentage of the recaptures. Within this radius are to be found the rivers which were also available to the fish of the earlier Moray Firth experiment, but from results which I shall mention shortly it is clear that many of the fish belonged to two rivers (Brora and Helmsdale) situated only a few miles on either side of the netting stations. The only important long journeys were made by one fish which went by the north coast to Lochinver on the west coast and four fish which travelled down the east coast, the extreme southern limit being the Yorkshire shore.

A still more restricted range of movement was shown by salmon (Fig. 10) marked in 1920 close to the mouth of the river Thurso in Thurso Bay near the east end of the north coast. Although, owing to a drought of over three months duration when they could not enter fresh water, they had every opportunity of spreading for long distances had they so wished, 59 out of 65 recaptures were made within five miles of the place of marking, and this not because the work was limited to a very short period or because the nets within this area were exceptionally numer-

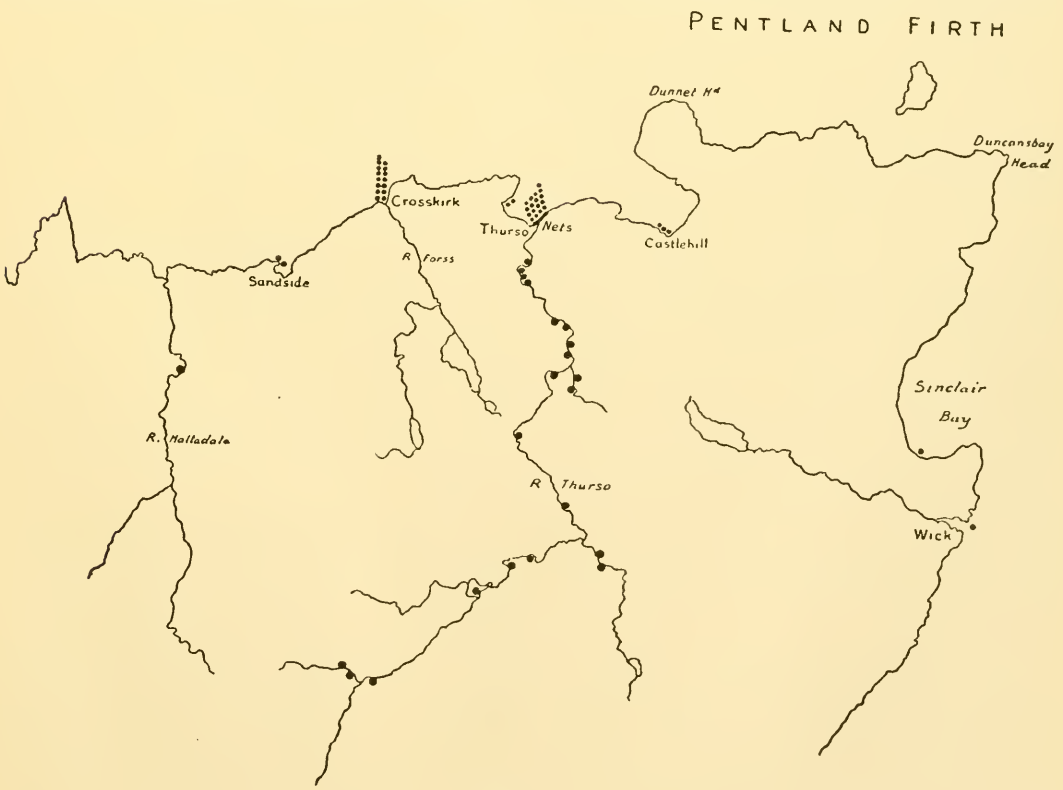

FIG. 10.

FIG. 11. MIGRATIONS OF SALMON MARKED AT STAVØY, AGDENES, NORWAY, IN 1936. (FROM DAHL AND SØMME.)

ous. Marking continued from May to September and the number of nets in the neighborhood was considerably less than in any part of the Moray Firth. This last experiment, and the Moray Firth results in general, have been strikingly confirmed by the marking station at the mouth of the Trondheim Fjord (Fig. 11) from which only two fish have been recaptured a few miles on the sea side of the fjord and all the rest actually in the fjord itself or in a river running into it.

This series of experiments in the northeast side of Scotland and in Norway seem to show that once the salmon, many of which on certain parts of the coast may be on passage, have reached the neighborhood (within 40 or 50 miles) of their destination they are prepared either to proceed straight up the river or to remain within the distance indicated, or a shorter distance, of the river until such time as they are able to go upstream. And the closer they get to the river mouth the shorter will be their migrations while so waiting.

The whole of the experiments are not by any means inconsistent with a feeding ground for the salmon at some indeterminate distance to the west of Norway and Great Britain from which an easterly migration takes the fish to the coasts after their feeding period is finished. On the Norwegian coast the fish spread either north or south to the final river, but it is possible that some Scottish fish may pass to the north of the country and touch Norway before they reach

Scotland, just as some Norwegian fish may arrive at the Scottish coast before they cross back to Norway. The majority of the salmon destined for the rivers of the east coast of Scotland and England would seem to enter the North Sea more probably north of Shetland or by the Fair Island channel rather than by the Pentland Firth, or more fish would be seen and would be caught in the neighborhood of the latter narrow channel. After they have entered the North Sea, enough evidence has not yet been accumulated to show whether the majority proceed direct to the neighborhood of their river or whether they do so by a circuitous route which leads first down the deeper waters away from the coast and then upwards from a more southerly position than their final destination. Some returns of fish marked as kelts and recaptured when clean, to which I have not referred in detail in this paper, would suggest the latter course as a possibility for at least some fish belonging to the more northerly Scottish rivers. Other evidence, to which I am also not able to refer here, suggests that even the farther travelled Scottish fish are returning to their native rivers and are not making a merely chance migration to an indefinite destination.

Summary

1. The salmon of the rivers emptying into the Baltic Sea migrate to its southern part, where they feed, and whence they return to their rivers as grilse, or older fish.

2. Salmon marked on the northwest and at the west end of the north coast of Scotland for the most part moved north and east, some going down the east coast or even crossing the North Sea to Norway. Comparatively few moved southward on the west coast and to no great distance.

3. Salmon marked on the west coast of Norway moved as far south as the Swedish coast and as far north as the White Sea, with some crossing southwestward to Great Britain.

4. Salmon in the Baltic migrate as far as 800 miles, and on the European coast as far as 1,600 miles. The apparent rates of travel are greater to distant places, and the average rate may be as high as 45 miles, or perhaps even 60 miles per day.

5. The facts are not inconsistent with a feeding ground for salmon at some indeterminate distance to the west of Norway and Great Britain.

References Cited

Alm, Gunnar. 1934. Salmon in the Baltic Precincts. Rapports et Proces-Verbaux des Reunions. International Council for the Exploration of the Sea. Vol. XCII.

Calderwood, W. L. Fisheries, Scotland, Salmon Fisheries. 1913, I; 1914, III; 1915, I; 1921, I; 1922, I.

Dahl, Knut and Sømme, S. Experiments in Salmon Marking in Norway, 1935; 1936; 1937. All in the series Skr. utg. av. Det Norske Vid.-Akd. i Oslo. I Matem.-Naturv.

Menzies, W. J. M. Fisheries, Scotland, Salmon Fisheries, 1937, I; 1938, I.

All papers by Calderwood and Menzies are in the Salmon Fisheries Series of the Fishery Board for Scotland.

THE ATLANTIC SALMON OF THE GULF OF ST. LAWRENCE

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THE Gulf of St. Lawrence is bounded on the east by Newfoundland, on the south by Nova Scotia, on the west by New Brunswick and Quebec, and on the north by Quebec. It is connected with the Atlantic Ocean on the north by the Strait of Belle Isle, between Newfoundland and Labrador, and on the south by Cabot Strait, between Newfoundland and Cape Breton. Because of the importance of its salmon fisheries, the multiplicity of its famous salmon rivers, the varied characteristics of its salmon, and its geographical situation the Gulf of St. Lawrence offers an excellent field for the study of the Atlantic salmon.

The depletion of the supply of salmon has become in recent years a topic of popular interest among all classes of salmon fishermen. The shore fishermen are vitally concerned with the welfare of the commercial fisheries, and the anglers and river men are deeply interested in the maintenance of the salmon rivers. Likewise, the perpetuation of the salmon stock is of considerable importance to the provincial governments, which not only derive directly a large revenue through the leasing of rivers to anglers, but also benefit indirectly through the employment of many of their citizens who cater to the anglers and participate in the commercial salmon fisheries.

While there is considerable difference of opinion as to whether or not a widespread decline is under way, since adequate statistics are lacking, nevertheless there are disconcerting instances of local diminution. The recognition that the early institution of practical methods of conservation may prevent a serious diminution of the salmon fisheries, and that effective measures depend upon an accurate knowledge of the local habits and movements of the salmon resulted in the inception of a general investigation of the salmon of the Gulf of St. Lawrence in 1937, when a series of cooperative tagging experiments was undertaken by Newfoundland, Canada, and the Province of Quebec. These experiments had as their objectives the tracing of the progress of the salmon in their general and local onshore movements during their spawning journey toward the rivers, and the determination of the characteristics which differentiate the salmon of the various sections of the Gulf of St. Lawrence. The facts presented in this paper have been derived from these experiments and from previous studies by the writer of the characteristics of the salmon of the various sections of the Gulf of St. Lawrence during the years 1930 to 1937 inclusive.

The salmon of this region remain from two to five years as parr in the rivers. Except for occasional captures during their pre-grilse life, little is known of their oceanic habitat after they leave the rivers as smolt. During this period it is possible that they may remain in the Gulf of St. Lawrence or that they may migrate to great distances in the ocean. Various theories have been offered, one of the most plausible being that the salmon frequent the slopes of the North Atlantic offshore banks. After having spent one, two or three years in the sea, they return to the coastal waters in May and June in order to enter the rivers in the late spring, summer and fall for the purpose of spawning about the first of November. The salmon are first observed in the vicinity of the Gulf of St. Lawrence in the Port-aux-Basques drift-net fishing area on the north side of Cabot Strait in early May. During the last of May they appear off the New Brunswick and Quebec shores,

where the peak run of the two-year sea-life salmon occurs three weeks later than at Port-aux-Basques.

The salmon probably follow definite routes of migration in the Gulf of St. Lawrence. Therefore, it is important to know whether the commercial drift-net and shore-net fisheries are so situated along these routes as to take an excessive number of salmon bound for definite sections of the coast, thereby producing by overfishing a diminution of the local supply. Effective measures for salmon conservation depend essentially on a thorough knowledge of their habits and characteristics.

The much disputed question of whether or not the salmon returns to spawn in the same river where it spent its life as a parr, irrespective of the mechanism governing its return, is not only of academic interest, but is of practical importance for the conservation of the salmon stock of individual rivers. The facts presented in this paper do not directly touch upon this question; nevertheless, since they are concerned with the characteristics and movements of the salmon in the coastal areas of these rivers, they have an almost equally important bearing upon the problem of salmon conservation.

Salmon Cycles

In 1931 Huntsman (1) and Phelps and Belding (2), independently and from entirely different data, discovered that there was a ten-year cycle of abundance in the salmon of North America with its peak on the years ending in five and its low point on the years ending in zero. The causes of this cyclic phenomenon, which is similar to that reported in other wild animals by several investigators, are still a matter of conjecture, although several apparently well-founded theories have been advanced. These cycles of abundance are chiefly responsible for our inability to determine accurately from the statistics of the commercial fisheries the inception of a general decline in the salmon stock, since the cyclic phenomenon tends to mask any immediate diminution and necessitates dealing with periods of 10 or even 20 years before reliable conclusions may be drawn.

In addition to cycles in abundance there are annual fluctuations in the weight of two-year sea-life salmon, the predominating sea-life class. These annual fluctuations follow an erratic six-year cycle and a long-term cycle of about 45 years. Such cycles are not primarily concerned with the salmon themselves, but apparently are due to feeding conditions in the sea. The salmon of several rivers in different parts of the Gulf of St. Lawrence consistently show uniform annual variations of weight. Since these annual fluctuations in weight are not synchronous for the salmon of Canada and Great Britain, it would seem reasonable to assume that the salmon of the two hemispheres do not inhabit the same oceanic feeding grounds.

Salmon Characteristics

Considerable information has been compiled concerning the characteristics of the Atlantic salmon in various parts of Canada and Newfoundland. If due allowance is made for annual and other variations, the aggregate of these characteristics provides a reasonable measuring rod for distinguishing the salmon of one locality from those of another. The most important differential characteristics are: (1) the proportion of large three-year sea-life maiden salmon; (2) the percentage of previously spawned salmon; (3) the duration of river-life, and (4) the length of two-year sea-life maiden salmon.

The salmon of the Gulf of St. Lawrence vary in their characteristics, which are distinctive for special sections. Even greater differences in characteristics are found between the salmon of various rivers, a fact which has strengthened the belief in the existence of river varieties or races and in the return of a salmon to the river where it lived as a parr. The characteristics of the salmon of a particular locality are determined by the composite characteristics of the salmon of its several rivers. However, if the locality in question is not a terminus, all salmon taken within its confines will

not possess the characteristics of local salmon, since their ultimate destinations may be elsewhere.

Table I gives a comparison of the characteristics of the salmon of certain localities in the Gulf of St. Lawrence. The data for Nova Scotia and the north shore of the Gulf of St. Lawrence are meager.

The Bay of Chaleur, Gaspé Peninsula, the western section of the north shore of the Gulf of St. Lawrence and Nova Scotia have a high percentage of three-year sea-life salmon, while comparatively few of these large salmon are found on the east coast of New Brunswick, on the west coast of Newfoundland and in the eastern section of the north shore of the Gulf of St. Lawrence. The percentage of previously spawned salmon on the west coast of Newfoundland is much greater than that of the other localities. Individual rivers differ markedly in the percentage of previously spawned salmon; the Cascapedia has an average of 22 per cent and the Moisie 20 per cent, whereas the Upsalquitch has as low as 5 per cent.

The time spent as parr in the rivers, though subject to annual variations, is longest in the northern localities such as the Bay of Chaleur, Gaspé Peninsula and the north shore of the Gulf of St. Lawrence, and is shortest in the southern localities such as Nova Scotia.

The length of the two-year sea-life salmon, an important differential characteristic, is shortest on the west coast of Newfoundland and longest in the Bay of Chaleur and on the Gaspé Peninsula.

The salmon taken in the Port-aux-Basques drift-net fishing area resemble most closely those of the Miramichi drift-net fishing area and of the east coast of New Brunswick, but apparently represent a mixed stock of salmon bound for various localities.

TABLE I

CHARACTERISTICS OF THE SALMON OF VARIOUS SECTIONS OF THE GULF OF ST. LAWRENCE

Locality	Percentage of sea-life classes			River years (smolt age)	Mean length two-year sea-life salmon (cm)
	Two-year	Three-year	Previously spawned		
Port-aux-Basques, drift-net fishery	90.3	2.9	6.8	3.27	78.5
West Coast of Newfoundland	72.1	2.3	25.6	3.40	74.7
Nova Scotia	42.1	57.9	5.0	2.55	78.8
East Coast of New Brunswick, Miramichi district	83.9	1.2	14.9	3.03	77.3
East Coast of New Brunswick, Miramichi drift-net fishery	88.5	5.3	6.2	2.90	77.9
Bay of Chaleur	52.8	38.8	8.4	3.59	79.3
Gaspé Peninsula	68.1	26.1	5.8	3.60	79.1
Moisie River, north shore of the Gulf of St. Lawrence	20.5	59.8	19.7	3.34	77.0

Seasonal Runs of Salmon

There are two distinct runs of salmon, exclusive of grilse, in the Bay of Chaleur and on the Gaspé coast: (1) the run of large salmon and (2) the run of small salmon. There is only one run, that of small salmon, in the Miramichi River, in the Miramichi drift-net fishing area, and in the Port-aux-Basques (Newfoundland) drift-net fishing area. Apparently the western section of the north shore of the Gulf of St. Lawrence has both large and small salmon, and the eastern section has small salmon only.

The large salmon differ from the small salmon by (1) their sea-life age and (2) the time of run. The division into the two groups of large and small salmon is primarily concerned with the maiden salmon, since the previously spawned salmon constitute only about 8 per cent of the stock. The small salmon, which average between 10 and 11 pounds, have spent two years in the sea; and the large salmon, which average about 21 pounds, have had three years of sea life.

The time of run of the large salmon in the Bay of Chaleur and on the Gaspé Peninsula, as shown in Table II, is about two weeks earlier than that of the small salmon. The time of run of the salmon in the Miramichi area on the east coast of New Bruns-

TABLE II

THE SEASONAL RUN OF SALMON (AVERAGE PERCENTILE DISTRIBUTION FOR 1930, 1931 AND 1937)

Weekly period	Large salmon	Small salmon		
	Bay of Chaleur and Gaspé Peninsula shore-net fisheries	Bay of Chaleur and Gaspé Peninsula shore-net fisheries	Miramichi drift-net fishery	Port-aux-Basques drift-net fishery (1937)
May 4–10				3.6
May 11–17				2.6
May 18–24	5.5	0.8	0.6	12.8
May 25–31	13.6	4.2	3.7	*33.5*
June 1–7	*29.2*	12.4	9.0	31.0
June 8–14	20.0	17.2	15.9	13.5
June 15–21	16.6	*24.1*	*20.8*	3.0
June 22–28	8.2	18.5	16.8	
June 29–July 5	4.6	12.3	10.8	
July 6–12	1.7	7.4	8.0	
July 13–19	0.4	2.6	6.8	
July 20–26	0.1	0.4	3.8	
July 27–August 2	0.1	0.1	3.8	
Total	100.0	100.0	100.0	100.0

wick in both the shore-net and the drift-net fisheries is practically identical with that of the small salmon in the Bay of Chaleur and on the Gaspé coast, whereas the Port-aux-Basques run of salmon is about three weeks earlier.

The source of the large salmon of the Bay of Chaleur and of the Gaspé coast is unknown. Except for a few stragglers in the early part of the season they do not pass through the Miramichi or the Port-aux-Basques drift-net fishing areas during the period of commercial fishing. These large salmon may have been in the vicinity of Port-aux-Basques before weather conditions permitted fishing, and in the Miramichi drift-net fishing area before the commercial season opened. It is possible, though unlikely, that the use of a $6\frac{1}{2}$-inch mesh in drift-net fishing may permit the escape of the large salmon.

From a practical standpoint the absence of large salmon in the commercial drift-net fishery is a most important factor in any consideration of the effect of the Miramichi and the Port-aux-Basques drift-net fisheries upon the angling and shore-net fisheries of the Bay of Chaleur and of the Gaspé coast. These two fisheries do not cause any serious depletion of the large salmon stock, but do take their toll of the supply of small salmon.

TAGGING EXPERIMENTS

In 1937 the movements of the salmon in the Gulf of St. Lawrence were studied by means of tagging experiments. The principal stations for tagging were: (1) Port-aux-Basques drift-net fishing area on Cabot Strait; (2) Margaree Harbor, Nova Scotia; (3) Miramichi drift-net fishing area on the east coast of New Brunswick; (4) Petit Gaspé; (5) Seven Islands; (6) Natashquan; (7) St. Augustin, and (8) St. Paul, the last four being on the north shore of the Gulf of St. Lawrence.

For the first time the tagging of salmon taken in the drift-net fishery was successfully accomplished, 75 to 80 per cent of the catch of the experimental boats being suitable for tagging. Thus an opportunity was afforded for tagging salmon when they first appeared early in the season at Port-aux-Basques in the southeastern part of the Gulf of St. Lawrence. It also provided a means of detecting the ultimate distribution of the Port-aux-Basques and Miramichi drift-net fishing area salmon and thus of determining the effect of drift-net fishing upon the shore and river fisheries of certain sections of the Gulf of St. Lawrence.

The percentages of recaptures for the various tagging stations are given in Table III. These data indicate that the percentage of recaptures is lowest when the dispersal is most widespread, *e.g.*, Port-aux-Basques, and increases proportionally as the distribution becomes more and more localized, the highest returns being obtained in the restricted area of Gaspé Bay.

Two general conditions are shown by the tagging experiments in the different sections of the Gulf of St. Lawrence: (1) the widespread dispersal of the salmon to all parts of the Gulf of St. Lawrence from the

TABLE III

PERCENTAGE OF TAGGED SALMON RECAPTURED IN THE GULF OF ST. LAWRENCE IN 1937

Locality of tagging	Character of the locality of tagging	Number of tagged salmon	Percentage of recaptured tagged salmon	Type of distribution
Port-aux-Basques, N. F. drift-net fishery	North side of Cabot Strait, 2–9 miles offshore	599	13.3	Wide radiating dispersal
East Coast of New Brunswick, Miramichi drift-net fishery	East Coast of New Brunswick, 4–15 miles offshore	411	17.5	Extensive coastwise range
North Shore of the Gulf of St. Lawrence (several localities) shore-net fishery	Indented coast and estuaries, onshore	337	20.2	Local coastwise
Margaree Harbor, N. S. shore-net fishery	Small harbor on open coast, onshore	267	28.7	Local coastwise
Gaspé Bay, P. Q. shore-net fishery	Entrance to large bay, onshore	100	38.0	Chiefly local in Gaspé Bay
Total		1,714	18.9	

Port-aux-Basques drift-net fishing area, and (2) the local nature of the movements of the salmon in most other localities.

The Port-aux-Basques drift-net fishery salmon were recaptured in Cape Breton, on the east coast of New Brunswick, in the Bay of Chaleur, on the Gaspé Peninsula, on the western part of the north shore of the Gulf of St. Lawrence, and on the west and south coasts of Newfoundland. In this widespread radiating distribution, one-sixth of the recaptured Port-aux-Basques salmon were taken outside the Gulf of St. Lawrence. The distribution of the salmon was 40 per cent to Newfoundland and 60 per cent to Canada.

Tagged salmon were taken in all sections of the Gulf of St. Lawrence except in the eastern section of the north shore, and showed the greatest concentration on the east coast of New Brunswick and in the Bay of Chaleur. Their absence in the eastern section of the north shore of the Gulf of St. Lawrence and the late run of salmon to that locality suggests the probability that the salmon of that section and of the northern part of the west coast of Newfoundland may come through the Strait of Belle Isle. The salmon tagged at Seven Islands likewise showed a widespread distribution covering the Bay of Chaleur and the western section of the north shore of the Gulf of St. Lawrence.

With few exceptions the salmon tagged at Margaree Harbor, Gaspé, Natashquan, St. Augustin, and St. Paul were recaptured locally and did not migrate to other sections of the Gulf of St. Lawrence. In addition to a localized distribution in these terminal areas there was lateral movement along the coast in both directions from the point of tagging, in each instance the trend being predominantly in one direction. Tagging in the estuaries of the St. Paul and St. Augustin rivers showed irregular movements up and down stream from the point of tagging, and even departures from the river.

The Miramichi drift-net fishery salmon showed a wide local distribution limited to the east shore of New Brunswick and the Bay of Chaleur, extending from Kouchibouguac Beach, N. B., to Gascons, P. I., at the northern limits of the Bay of Chaleur. Slightly over one-half of the salmon, other than those recaptured in the drift-net fishery, went to the Bay of Chaleur. The distribution of the tagged salmon corroborated

the conclusions of Phelps and Belding (3) in 1930 as to the ultimate destination of the Miramichi drift-net salmon.

The results of the tagging experiments illustrate the general effect of the Port-aux-Basques drift-net fishery on the salmon of nearly all sections of the Gulf of St. Lawrence and the local effect of the Miramichi drift-net fishery on the salmon of the east coast of New Brunswick and the Bay of Chaleur. Likewise the early arrival, the few local recaptures and the wide distribution of the Port-aux-Basques salmon suggest but do not prove that these salmon are entering the Gulf of St. Lawrence from the ocean.

Summary

1. There is a ten-year cycle of abundance in the Atlantic salmon of the Gulf of St. Lawrence, which attains its peak on the years ending in five and its low point on the years ending in zero. This cyclic phenomenon tends to mask evidence of a possible decline in the commercial fishery.

2. The salmon of the various parts of the Gulf of St. Lawrence differ in such characteristics as (1) the proportion of three-year sea-life maiden salmon, (2) the percentage of previously spawned salmon, (3) the duration of river life, and (4) the length of two-year sea-life maiden salmon. The aggregate of these characteristics may provide a means of differentiating the salmon of various localities.

3. Exclusive of grilse there are two runs of salmon in the Gulf of St. Lawrence: (1) the run of large three-year sea-life salmon and (2) the run of small two-year sea-life salmon. The peak of the large salmon run occurs about two weeks earlier than that of the small salmon. The large salmon are found in appreciable numbers only in the Bay of Chaleur, on the Gaspé Peninsula, on the western section of the north shore of the Gulf of St. Lawrence and on the Cape Breton coast.

4. In 1937 the movements of salmon in the Gulf of St. Lawrence were studied by tagging salmon taken in shore-nets and drift-nets. For the first time, salmon were tagged successfully after capture in gill-nets.

5. The average percentage of recaptured salmon tagged at eight stations in various parts of the Gulf of St. Lawrence was 19.4 per cent. The percentage of recaptures increased as the range of distribution decreased, the highest returns, 38 per cent, being obtained from tagging in Gaspé Bay and the lowest returns, 13.3 per cent, from tagging in Cabot Strait.

6. The salmon tagged at Port-aux-Basques on the north side of Cabot Strait showed a widespread distribution to all parts of the Gulf of St. Lawrence except the eastern section of the north shore between Natashquan and the Strait of Belle Isle. About three-fifths of the recaptured tagged salmon were taken in Canada and two-fifths in Newfoundland.

7. There appears to be a definite westward movement of salmon from Cabot Strait to the western shores of the Gulf of St. Lawrence.

8. The recaptured salmon tagged at the Miramichi drift-net fishery on the western shore of New Brunswick were equally distributed between the Bay of Chaleur and the east coast of New Brunswick.

References Cited

1. Huntsman, A. G. 1931. The Maritime Salmon of Canada. *Bull. Biol. Bd. Can.*, XXI.
2. Phelps, E. B., and Belding, D. L. 1931. A Statistical Study of the Records of Salmon Fishing in the Restigouche River. Privately printed.
3. Phelps, E. B., and Belding, D. L. 1930. An Investigation of Certain Conditions Affecting the Salmon Fisheries of the Bay of Chaleur and Adjacent Waters. Privately printed.

MIGRATION AND CONSERVATION OF ATLANTIC SALMON FOR CANADA'S MARITIME PROVINCES

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THE view that the salmon migrates from its river far out into the ocean to specific grounds in order to find abundant food, and that at the appointed season it migrates back by instinct to its river in order to spawn is simple, clear-cut and in accordance with certain well-established facts. Salmon do leave the rivers, do grow rapidly and become fat in the sea, do return to the rivers at rather definite seasons and do spawn in the rivers after return. The history of knowledge shows us, however, that the simple and obvious interpretation of the facts may, with fuller knowledge, have to be modified or abandoned, and that things are much more complex than they at first appear to be. That the earth is flat and that the sun rises in the east and sets in the west seem so simple and in accordance with fact that not a few people still refuse to accept the more complicated conception of a spherical, rotating earth, one of quite a number of planets in a system, of which the sun is the center. Scientists, however, insist that with all the facts the conception of the solar system is necessary.

The facts that have been accumulating in relation to the Atlantic salmon of the Canadian Maritime provinces have forced me to abandon or modify the simple view of salmon migration and to realize that the salmon's movements form a very complicated picture. Some salmon do not leave the river system, most of them seem not to go far out in the ocean, there seem to be no specific feeding grounds, the time of return to fresh water varies greatly with conditions and quite a considerable number of the salmon from some rivers scatter widely and may enter very distant rivers.

It has been customary to refer such diversity in behavior to differences in the nature of the salmon, that is, to differences in racial inheritance. However, the *structural peculiarities* that have been relied upon to distinguish races are being shown one after the other to be produced by differences in environment during the development of the individual, and, therefore, not to be heritable. Like the structural peculiarities, the *differences in behavior* are themselves proving to be related to environmental differences. In a recent experiment (White and Huntsman, 1938) the fry from Restigouche River salmon, which return to the river principally *after two* or *three years* in the sea, many of them *early* in the season, were planted in the east branch of the Apple River at the head of the Bay of Fundy. Their behavior was indistinguishable from that of the local salmon, for they returned to the river almost wholly as grilse, that is *after one year* in the sea, and *only late* in the season. That the environment alters behavior is undoubted. It has yet to be proved that there are differences in behavior of the Atlantic salmon that are heritable.

This recently developed view of the importance of the environment in determining the behavior of the salmon has now made it necessary to study the physical conditions to which the salmon of any particular river are exposed, if one is to expect to be able to understand their behavior. The burden of work for the investigator is a heavy one, since the difficulty of following the salmon's movements is great enough without having to procure data on the various factors that may affect those movements. Progress must inevitably be

rather slow and the developing picture continue to be fragmentary.

The St. John Salmon

The St. John River (Fig. 1) drains western New Brunswick and has as its principal branch for salmon, the Tobique River of the northern part of the province. Although the salmon are unable to ascend beyond Grand Falls, the whole river has a very large watershed, extending into the high land of northern Maine and southern Quebec, and assuring a large and quite dependable discharge, which is made a steadier one by being to some extent stored at sea-level in a very extensive estuary. The very narrow mouth of the estuary at St. John harbor not only holds the river water back, but also prevents the entrance of much sea water from the Bay of Fundy

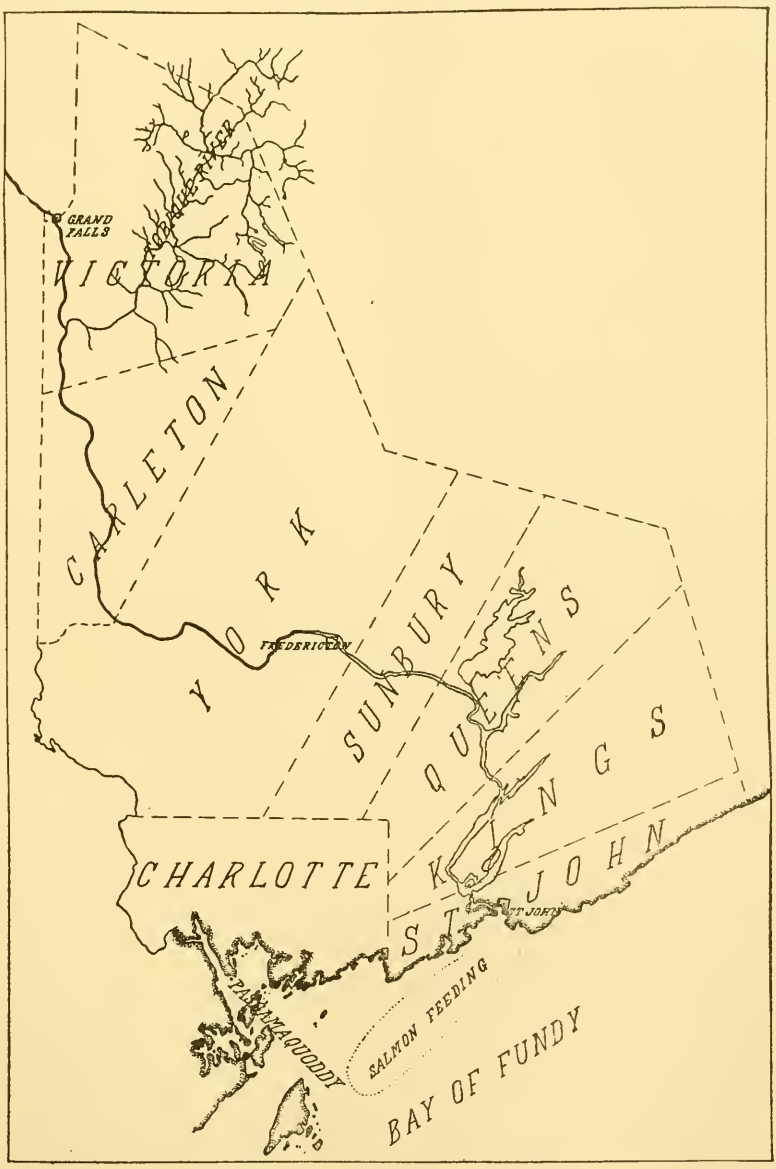

Fig. 1. St. John River, New Brunswick, showing distribution of salmon from feeding grounds in the Bay of Fundy to uppermost spawning grounds in the Tobique River.

and produces at this point a reversing falls, the fresh water falling out only when the water of the bay is below half-tide level. The discharge, although intermittent, is so great that there is a continuing zone of river influence from the harbor mouth southwestward along the coast for about 50 miles to the Passamaquoddy region, where it is dissipated in the strong tidal mixing of the archipelago there.

This peculiar physical background is associated with a definitely limited sea movement of the salmon. The salmon, when near the end of their first summer in the sea and around a pound in weight, are taken quite regularly, sometimes in very considerable quantities, in the herring or "sardine" weirs from just outside St. John harbor to the island of Grand Manan just outside the zone of river influence. These facts indicate that, although the smolts descend the river for as much as 175 miles, and pass through 70 miles of estuary, they are when half-way to becoming grilse from three to perhaps 50 miles from the mouth of the estuary and definitely related to the zone of river influence. In this zone there is an abundance of food, consisting of pelagic crustacea of various kinds and small fishes. We may reasonably conclude that these small salmon are like the herring in being liable to capture in the weirs only when roaming about, that is when not feeding, and when the temperature is not too low (Huntsman, 1933). At any rate, the time of the year when they are taken is around September, when growth (and presumably feeding) slackens and the temperature is highest.

In the following year, as grilse, they are taken in the weirs (the drift-nets are of too large a mesh) from St. John harbor to Grand Manan. They are taken principally at St. John, where they are nearly all males, appear as early as June, and increase in numbers during the summer. A fair number enter the estuary, ascend the river and spawn in the fall. About November, quite a number of others, practically all females about 9 lb. in weight and immature, begin to enter the estuary, and the run continues till stopped by the cold in early January. These remain in the deeper parts of the estuary toward its inner end, and ascend the river in the spring, starting about the middle of May. At this same time the main mass of the salmon out in the bay in the zone of the river influence start to move, first near St. John. They are about 11 lb. in average weight and principally females, and they enter the estuary and ascend the river. They are feeding on the local shrimp (Euphausiids) and small herring, increase in weight with the season, become most numerous toward the end of June or early in July, and as maturing salmon are taken with drift-nets of suitable mesh in St. John harbor and throughout the zone of river influence in the bay and only rarely outside this.

Tagging experiments being made this year are already showing that these salmon do not leave the zone of influence of the river, but move to and fro in it, going from the harbor outwards towards the extremity of the zone as well as inwards to the mouth of the estuary. There is not the steady movement riverward that theorists have led us to expect.

When these salmon, after being spawned in the autumn are liberated just outside the harbor, they enter the estuary, so far as can be judged by recaptures. They occur as kelts the next spring, as clean fish during that summer, and as clean fish in the summer following, from the harbor through the estuary and up the river. Very few are found in the bay, and only in the second year; likewise they are found far up the river only in the second year. In their phenomenal inward distribution these large fish exhibit a marked contrast with the small salmon or post-smolts found only in the bay and toward the outer end of the zone of river influence.

The Miramichi Salmon

The Miramichi salmon (Fig. 2) liberated as kelts in the Northwest Miramichi estuary (not outside the estuary as were the St. John kelts), show a distribution as kelts the next spring similar to the St. John fish, from some distance up the river down through the estuary to its mouth. As clean

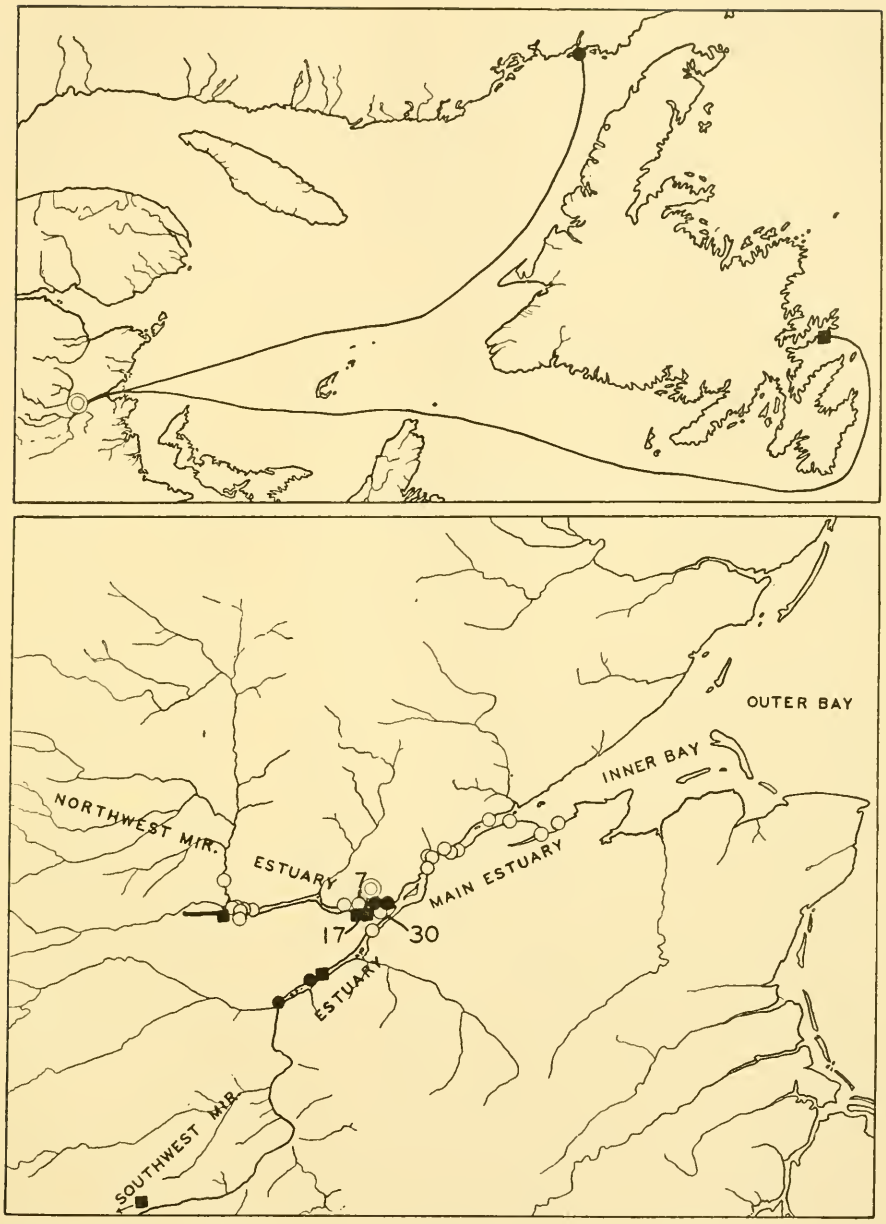

FIG. 2. DISTRIBUTION OF RECAPTURES OF SALMON LIBERATED AS KELTS IN THE ESTUARY OF THE NORTHWEST MIRAMICHI RIVER, NEW BRUNSWICK. LOWER—LOCAL RECAPTURES AS KELTS (PLAIN CIRCLES), AS CLEAN FISH IN THE FIRST YEAR (SOLID CIRCLES), AND AS CLEAN FISH IN THE SECOND YEAR (SOLID SQUARES). UPPER—DISTANT RECAPTURES.

fish during the first and also the second summer, however, they are farther in, none being taken in the outer waters, where the bulk of the virgin fish are captured, or even in the main estuary. Being taken chiefly in the fall, some would surely be captured in the outer waters if they came in from the Gulf of St. Lawrence. The conclusion that these do not leave the estuary seems unavoidable.

This must be qualified since, unlike the St. John fish, a very few of the Miramichi

salmon, tagged as kelts, have been found in other regions. These have been taken only far away, outside the Maritime provinces, one in the first year following liberation, at Bonne Esperance on the north shore of the Gulf of St. Lawrence near the Strait of Belle Isle, and the others on the east coast of Newfoundland. The conclusion seems necessary that most of the Miramichi salmon, like all those of the St. John, are definitely held by river influence well into the estuary, but that occasional individuals are carried outside the zone of this influence (whose extent is undetermined, but well out into the Gulf), and to very distant places. Known currents will carry these salmon out of the Gulf through Cabot Strait, but, if they crossed Cabot Strait, they would be carried inwards and up the west coast of Newfoundland to the Strait of Belle Isle.

Relation of Salmon to River Influence

The facts that have been given seem to show rather definitely that most of the salmon of a river are in the sea in relation to its zone of influence, and that, the larger they become, the farther are they in toward the river mouth, at least after they have been in the river for spawning. There is also an indication that some of the salmon may be carried far away from the river influence. These conclusions are at variance with the generally accepted theory that has already been outlined, and involve abandonment of the idea that the salmon undertakes definite purposeful migrations.

The order to be seen in the salmon's movements is of varied character. White (1936) found that Restigouche salmon planted in the east branch of the Apple River entered that branch alone until close to spawning time, as if tending to collect in the estuary of that branch rather than in the estuary of the south branch. There are facts to show that salmon tend to stay in the water from their river when it forms a more or less recognizable zone in the sea. The St. John salmon are virtually restricted to such a zone. The water from the Margaree River (Fig. 3) passes northward along the coast from the mouth of the estuary, but has only an intermittent influence. Nevertheless, the tagged fish, whether virgins or kelts, are captured chiefly along the course of this influence, as are also the untagged fish of the commercial catch. How they recognize such water, we do not know.

Passive Transportation

Even without facts to demonstrate it, there would be a general willingness to believe that salmon can recognize river water; but there seems to be a general unwillingness to concede the probability that salmon are carried about in the sea by the currents. That a fish which ascends rapid

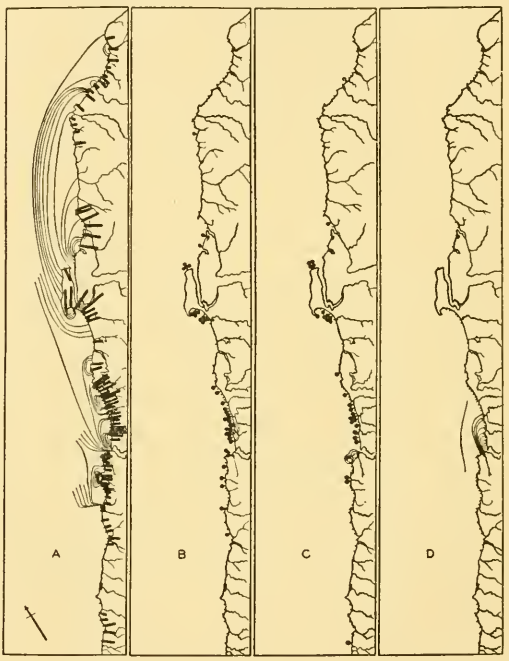

Fig. 3. The Margaree coast, showing relation of salmon to the river mouth (one-third the way up from the bottom) and to Cheticamp Island (over half-way up). A. Catches of salmon by individual nets in 1936, and order in commencement of fishery, the successive lines out from coast representing successive days. B. Recaptures in 1935, 1936 and 1937 of salmon liberated just north of river mouth. C. Recaptures in the same years of salmon liberated just south of river mouth. D. Distribution of surface water of low salinity with ebbing tide, going north from river mouth. The locations of the nets are shown.

streams and leaps falls should be determined in its distribution by the comparatively slow movements in the sea seems at first sight unlikely. Nevertheless the facts definitely indicate that such occurs. When the salmon are near the surface of the sea in summer, an onshore wind which drives the superficial water and heaps it against

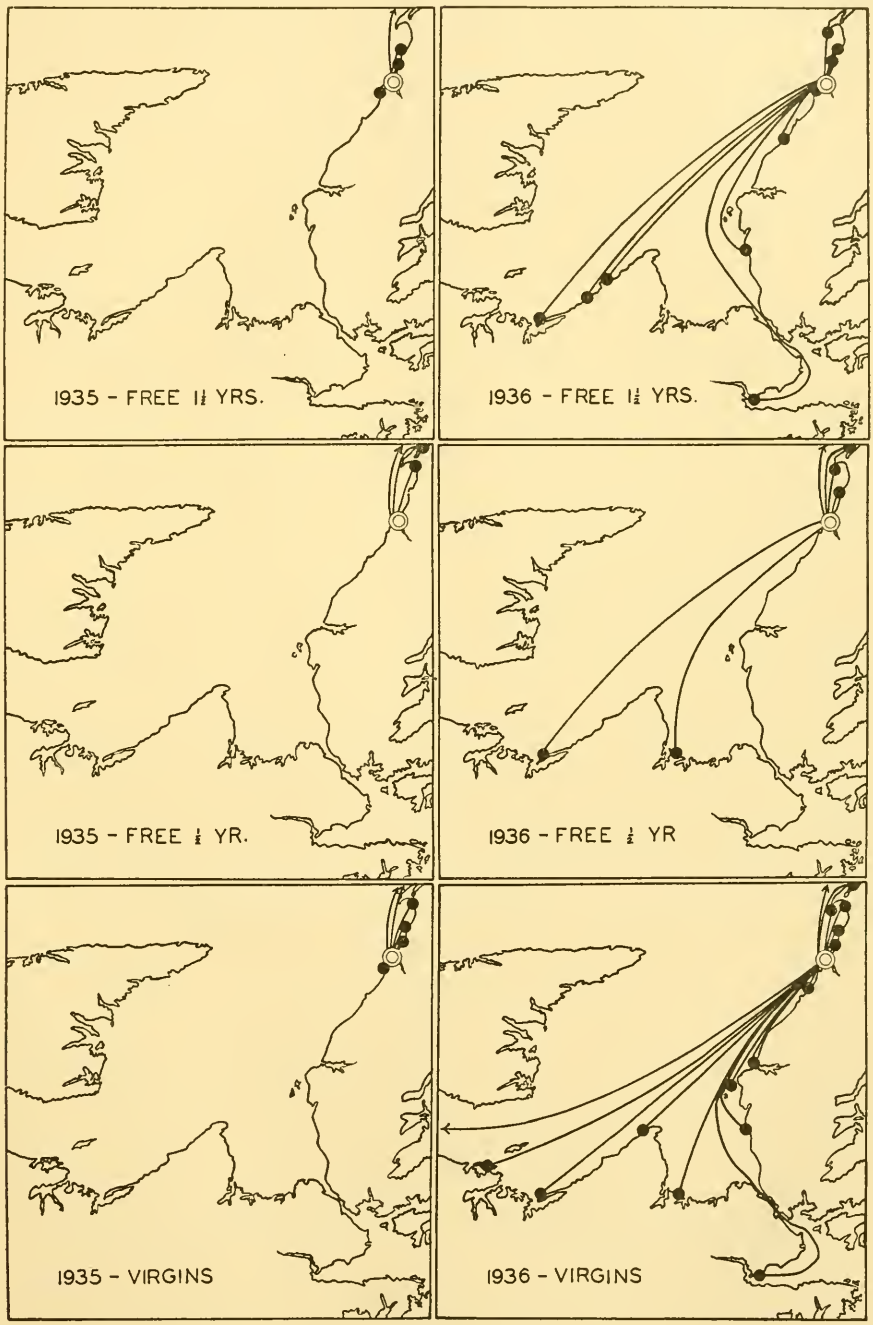

FIG. 4. RECAPTURES OF MARGAREE SALMON TO THE SOUTHWEST IN THE YEARS 1935 AND 1936, FOR COMPARISON. UPPER AND MIDDLE PAIRS—SALMON LIBERATED AS KELTS A YEAR AND A HALF AND A HALF YEAR PREVIOUSLY. LOWER PAIR—SALMON NEWLY LIBERATED AFTER CAPTURE AS VIRGIN FISH.

the Margaree coast, increases the catch of salmon by the coastal nets, as soon as the water becomes calm. In the zone of influence of the St. John River water in the Bay of Fundy, a southwest wind will concentrate the salmon toward the river mouth, as in the record catch of 713 salmon made there on July 30, 1935, of which 531 were taken by the Lorneville boats operating just outside the mouth of the harbor. That some condition such as current effects large scale movements of the salmon in the sea is

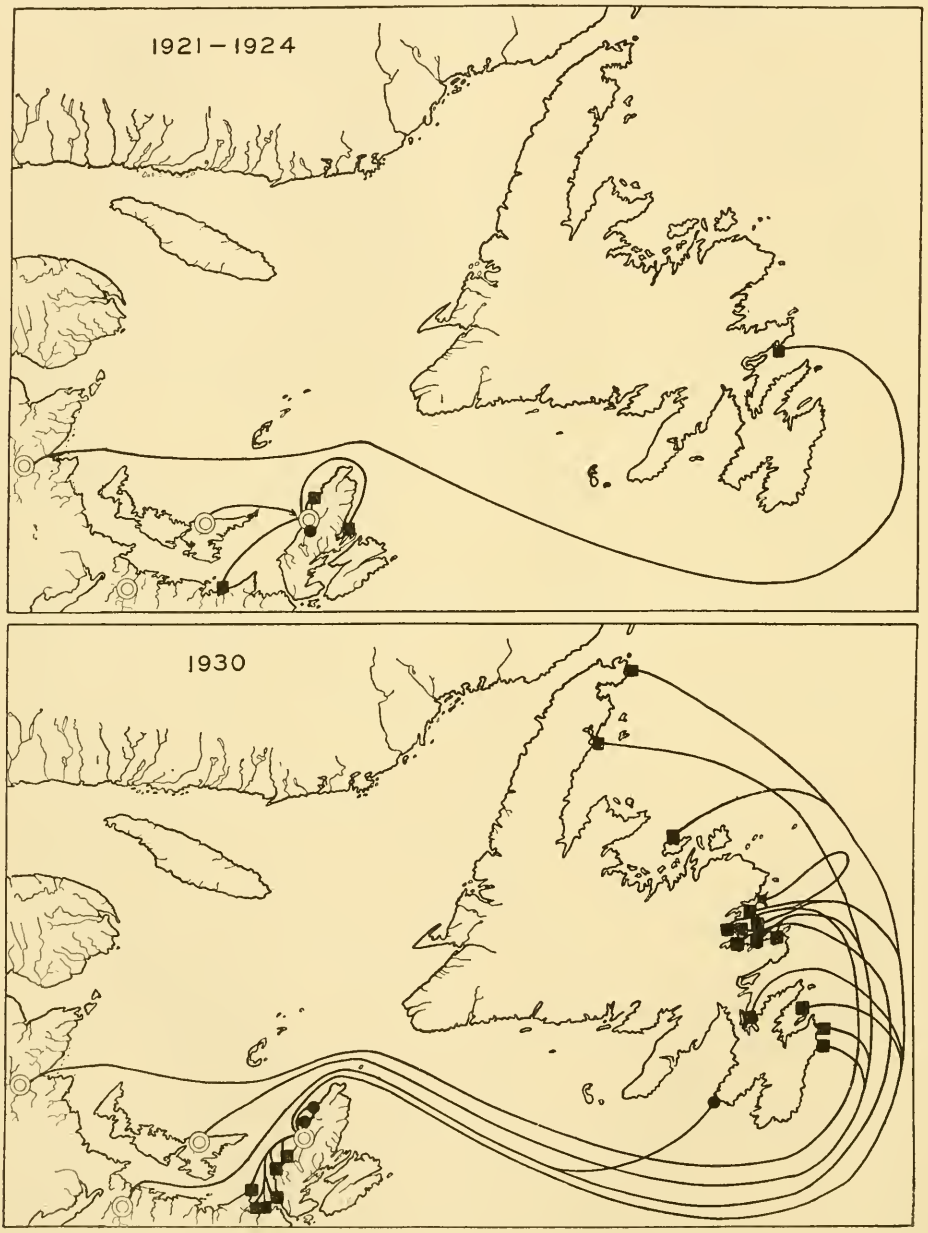

FIG. 5. COMPARISON OF DISTANT RECAPTURES OF SALMON LIBERATED AT SPAWNING TIME IN 1930 WITH THOSE LIBERATED FROM 1921 TO 1924, FOR THE MIRAMICHI RIVER, NEW BRUNSWICK, THE MORELL RIVER, PRINCE EDWARD ISLAND, THE PHILIP RIVER, NOVA SCOTIA, AND THE MARGAREE RIVER, CAPE BRETON ISLAND. APPROXIMATELY EQUAL NUMBERS WERE LIBERATED IN EACH PERIOD.

shown by the difference between 1935 and 1936 in the recaptures of Margaree salmon to the southwest of the river mouth (Fig. 4). In the summer of 1935 there were three lots of tagged Margaree salmon in the sea, those liberated as kelts a year and a half previously, those liberated as kelts a half year previously and virgin fish just liberated. The Margaree kelts, unlike those of the St. John and the Miramichi, are in the outer waters with the virgin fish. None from any lot were taken more than four miles to the southwest. In the summer of 1936, there were three comparable lots of tagged salmon in the sea, and from each lot there were recaptures 80 miles to the southwest nearly as far as Pictou, and from two of the lots also recaptures 95 miles away in Chedabucto Bay through the gut of Canso. Some condition such as current must have been responsible for such a peculiar movement of the Margaree salmon in 1936.

Another instance of peculiar movement, apparently attributable to current is the following. Margaree salmon tagged and liberated as kelts in various years from 1913 on had failed to give any recaptures from the east coast of Newfoundland, except one in the third year after liberation. Then of those liberated in the fall of 1930, six were taken on that coast in 1932. A similar condition (Fig. 5) obtained (1) for the Morell River, Prince Edward Island, with six recaptured on that coast in 1932, (2) for the Philip River, Nova Scotia, with one so recaptured, and (3) for the Miramichi River, New Brunswick, also with one recaptured. (Similar numbers liberated in these rivers from 1921 to 1924 failed to give any very distant recaptures except one for the Miramichi to the east coast of Newfoundland in 1924.) As all of these were liberated in the fall of 1930, it is to be concluded that they were affected by the same conditions, such as an unusual current, which may be presumed to have carried them out into the ocean and to the northeast so that, on moving into coastal waters characterized by river influence, they reached the east coast of Newfoundland.

There have been no recaptures of St. John salmon tagged as kelts and liberated outside the river mouth, except in the river and in its zone of influence in the sea. Contrasted with this the Annapolis salmon (Fig. 6), on the opposite side of the Bay of Fundy, when tagged as kelts and liberated far up the river, have been recaptured chiefly in two different places: (1) well up the river and (2) on the east coast of Newfoundland, 800 miles or more away. This extraordinary fact seems to find explanation only through currents. The Annapolis River has little recognizable influence outside the mouth of the Annapolis basin in the Bay of Fundy. Such of the Annapolis salmon as go so far are practically without river influence to hold them. The demonstrated circulation of the water is such as to carry them around (one was recaptured this year in the St. John outflow) and out of the bay into the Gulf of Maine, thence out into the Atlantic, and along a northeasterly course toward Europe. Along such a course, once Cape Sable has been passed, the nearest land is the east coast of Newfoundland. There they are taken in a year's time, in the late fall, a different time of year from that (the summer) in which the salmon from the rivers of the south side of the Gulf of St. Lawrence are taken on that east coast of Newfoundland. These instances of the relation of ocean currents to salmon movements should be sufficient to show the need for knowledge of the movements of the water if we are to understand the movements of the salmon.

Active Movements

The picture so far developed is (1) that the salmon becomes active as the water warms from the ice-cold condition of the winter, (2) that it roams chiefly when not engaged in feeding, (3) that it tends to stay in river water or the water of its own river, in preference to other water and (4) that it is carried in mass movements of the water. Are the active movements of the salmon when in the sea directed, or are they at random? The available evidence indicates that they are at random, except in a

FIG. 6. DISTANT RECAPTURES OF SALMON LIBERATED AS KELTS IN THE ANNAPOLIS RIVER, NOVA SCOTIA. LOCAL RECAPTURES WERE ALL IN THE RIVER. ALL RECAPTURES OF SALMON LIBERATED AS KELTS OUTSIDE THE MOUTH OF THE ST. JOHN RIVER ACROSS THE BAY OF FUNDY WERE LOCAL.

turbulent current. Flowing water with fine turbulences, that result from contact of the water with solid bodies, causes the salmon to orient itself against the direction of flow. With the strength of the current varying sufficiently from place to place, the salmon will come to rest in relation to the bottom where the strength of the current matches its activity. Tidal currents will not lead it very far, and, as the tide changes, the direction will be reversed. Currents issuing from rivers will lead it riverward. These features suffice to explain the behavior of salmon on the Margaree coast. They are taken first in the spring where the sea water has the best chance to become warm, the place where the water issuing from the extensive, shallow, Cheticamp harbor during falling tide collects with little dissipation by mixing, that is toward the mouth of the Cheticamp River (see Fig. 3). They tend to collect along the course taken by the water issuing from the Margaree River. They become concentrated near shore with onshore winds. Wherever they may be tagged and liberated, they go in every possible direction. They tend to collect inside projecting points of land, such as Cheticamp and Enragée points, where tidal currents do not run very strongly. Strong flow from the Margaree River leads them riverward.

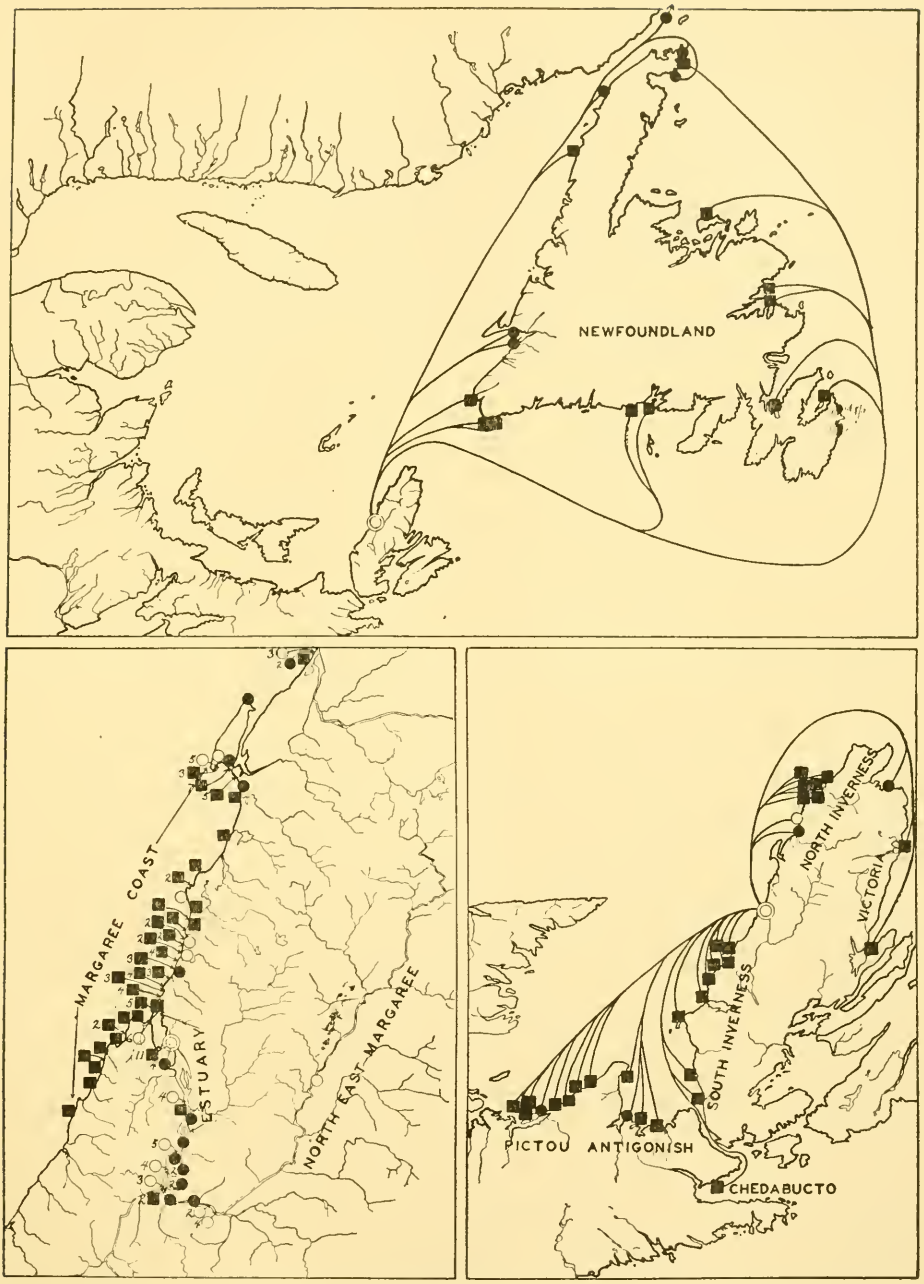

FIG. 7. RECAPTURES OF SALMON LIBERATED AS KELTS IN THE ESTUARY OF THE MARGAREE RIVER. LOWER LEFT—LOCAL RECAPTURES IN THE RIVER AND ON THE COAST NEAR THE RIVER MOUTH. LOWER RIGHT—MORE DISTANT RECAPTURES, BUT WITHIN RADIUS OF 100 MILES, ALL IN NOVA SCOTIAN WATERS. UPPER—RECAPTURES BEYOND 100 MILES, ALL IN NEWFOUNDLAND WATERS.

As the river influence is on the whole poor they are spread widely (Fig. 7) and go with ocean currents to distant places, from which their return is doubtful.

MORE RAPID MOVEMENT TO DISTANT PLACES

It is worthy of note that, just as these salmon tend to remain in the intermittent zone of influence of the Margaree River, so,

as active fish in the summer, they do not scatter widely and far as do salmon in ocean water entering the Gulf on the Newfoundland side of Cabot Strait (Fig. 8) but fail to leave the steady zone of influence of the St. Lawrence and associated rivers that fills the southern part of the Gulf and passes out through Cabot Strait along the Cape Breton coast. In this zone they move rather far and widely to the west and south, where there is no Margaree influence, but not quite so far to the north and east, whither the influence extends. In these movements to other districts, there is to be observed the phenomenon that Menzies (1937 and 1938) has described for salmon of the Scottish coast. Those showing

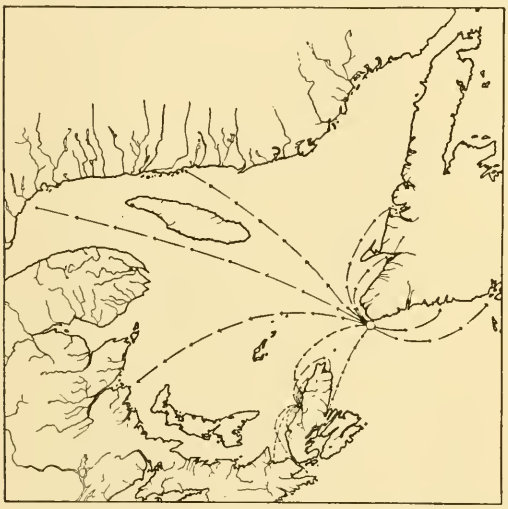

FIG. 8. FASTEST RATES OF TRAVEL OF SALMON TO VARIOUS POINTS AS LIBERATED IN 1937: (1) OFF PORT-AUX-BASQUES, NEWFOUNDLAND, AND (2) NEAR THE MOUTH OF THE MARGAREE RIVER, CAPE BRETON ISLAND. THE COMPARATIVE RATES ARE SHOWN BY THE LENGTHS OF THE ARROWS.

the fastest rate of travel to a distant district have a more rapid rate than those with the fastest rate to a nearby district. It might be thought that those going to distant districts travel more rapidly or do not linger on the way. But if caught at the beginning and again at the end of this course why should not some be caught on the way and upset the order? It may be as well to avoid unfounded assumptions and consider whether known things will not explain the phenomenon. Going out from shore, the circulation of the water, that is the long-term movement in one direction, becomes more rapid, *e.g.,* from two miles to four miles, to six miles, and even to eight miles per day as shown by drift bottles (Huntsman, 1924). Also, the salmon when near shore or bottom in turbulent tidal currents will orient itself and, where the strength of the current matches its activity, will come to rest in relation to the bottom. Therefore, those salmon that happen to wander farthest out from the coast will be carried most rapidly in the direction in which the water is circulating, and will have least opportunity to come to rest in relation to the bottom. I doubt that anything more is required to explain the more rapid rates shown by the salmon that reach distant districts.

MOVEMENTS IN THE RIVER

It is well established and well recognized that the young salmon (as smolts) and the spawned salmon (as kelts) descend rivers to the sea and that the sexually maturing salmon ascend rivers from the sea. It is not, however, generally appreciated that such directions of movement are far from being invariable. Depending upon the conditions with which they are faced, smolts and kelts will ascend as well as descend rivers, and sexually maturing salmon will descend as well as ascend. Nor is it that any physical difficulty prevents the usual behavior. It is clearly a matter of how the individual fish reacts to the conditions to which it is exposed. To understand the salmon's movements, it is necessary to understand both the way in which the fish reacts and what the conditions are.

As observed in the Margaree River the salmon parr when at least 4½-inches long in the spring transform into smolts as the temperature rises. This change in nature results in their tending to leave the bottom, coming nearer the surface under the same conditions of light and wandering rather than staying in rapid water. This results in their going downstream to the river estuary, where they collect. With springing tides which empty the estuary very

thoroughly with the ebb, they are swept out to sea.

The maturing salmon enter the Margaree estuary through its narrow mouth following a freshet, and ascend above the head of tide under the same stimulus, although how the freshet acts is not clear. They remain in the river only where they find pools of sufficient size, particularly in depth.

The smolt, the maturing salmon and the kelt differ somewhat in nature, as shown by the degree of response to changes in light and in current. The movement that results, whether upstream or downstream, depends not only upon the nature of the individual fish, but also upon the strength of the physical stimulus to which the fish is exposed. Only a small beginning has been made in finding out details of the reactions of the salmon and details of their physical environment, which are needed to explain the movements in the river.

Conservation

Presumably the conservation of salmon is for the purpose of assuring continued maximum exploitation of the salmon by man for food and sport. I do not know of any general desire to have them preserved either for man's pleasure in observing them, as seems to be true for birds, or for the maintenance of more desired forms of life, as fish-eating birds might be considered to be.

Conservation has received such general and strong advocacy that it is seemingly considered as desirable in itself apart from any object it may originally have had. That object should not be obscured or we may be defeating our own ends. It is a common mistake to generalize from a particular, unrepresentative case; salmon conservationists constantly base their efforts upon undoubted instances of man's having done away with the entire salmon stocks in certain rivers. The jump is then made to efforts towards conserving the general stock of salmon by restricting the netting of salmon in the sea, by which means it is true more salmon are captured than by angling in the rivers.

Such a procedure is decidedly unscientific. It is well known that for the most part each river has its own stock of salmon. For this reason each river stock should be considered by itself to ascertain (1) to what extent it is being exploited and (2) whether any proposed restriction of the fishery will permit a larger yield in the future. Until such questions are answered we may, if we restrict the fishery, be like the dog in the fable, "drop the meat to seize its reflection in the water." The unscientific character of vague statements that net fishing is endangering or will endanger the stock of salmon should be recognized. I have failed to find evidence that net fishing in the open sea or on an open coast has ever seriously reduced the stock of salmon, and I believe it fairly certain that such fishing would become quite unprofitable before there was serious reduction. In narrow estuarial waters and in the rivers, however, man can rather readily reduce the numbers of salmon to very low levels, and *there* is the place of danger. From the standpoint of mere conservation of the stock, it is desirable that the salmon should not enter the river until late in the season, unless they are less likely to perish there. However, for exploitation by anglers, they should enter early in the season. Any use, in argument for conservation, of the numbers of adult salmon taken by the commercial nets or in angling may be quite misleading, since the significant thing is reproduction, the number of salmon that remain for spawning, which may have a converse as well as a direct relation to the number removed by capture. Even the number of salmon entering the river is no safe criterion when the extent of poaching is not accurately known. The net fishery, when well and regularly prosecuted year after year, seems to give very good evidence of fluctuations in the stock, and accurate records of the catch in such fishery are procurable and valuable for following the fluctuations. Apparently, however, there can be wide fluctuations with always an ample number of spawning individuals. It is hardly wise to conclude that conservation

is necessary, until there are facts to prove that the stock is endangered.

The matter of maintaining the stock or actually increasing it is best handled by work in the rivers. For any particular river we should ascertain what suitable spawning beds are available, whether there are sufficient spawning salmon to utilize them properly, whether the young from natural spawning make proper use of the food available for them, and how the death of the young from enemies, disease, and physical or chemical causes can be prevented. Conservation of the maturing fish will be clearly advisable only when the numbers of spawning fish are found to be insufficient for proper utilization of the river's capabilities for natural smolt production.

Summary

1. The facts indicate a sea distribution of the salmon of the St. John River only as far out as about 50 miles from the river mouth into the Bay of Fundy, within which they are taken half-way toward becoming grilse. Tagged maiden fish remain within the zone of river influence and show no steady movement riverward, but movement outward as well as inward.

2. Tagged kelts, when liberated outside the mouth of the St. John River, showed a later distribution predominantly inward in contrast to that of the maiden fish. Those liberated in the estuary of the Northwest Miramichi River were later recaptured even farther inward in contrast with the maiden fish.

3. There is strong evidence that salmon are passively transported in the sea even to very great distances. Where river influence is slight and intermittent as for the Margaree River, Cape Breton Island, the salmon are widely scattered.

4. More rapid movement to distant places, which tagging experiments show, is explicable as resulting from the fish being farther out from the shore, in more rapidly moving water and away from turbulent current, in which they cease to wander.

5. Ascent or descent of a river by the salmon at any stage is seen as being variable and dependent upon its condition and upon the conditions surrounding it, and not upon its ability to achieve a purposeful migration.

6. The necessity for the conservation of the salmon stock of any river should be established before restricting its exploitation by man.

References Cited

Huntsman, A. G. 1933. Heat and Cold Make Herring Seasons in Passamaquoddy. *Atl. Progr. Rep. Biol. Bd. Can.*, 7: 3–6.

———. 1924. Circulation and Pollution of Water In and Near Halifax Harbour. *Contr. Canad. Biol.* N. S., 2: 69–80.

Menzies, W. J. M. 1937. The Movements of Salmon Marked in the Sea. I. The North-west Coast of Scotland in 1936. *Fish. Scot. Salmon Fish.*, 1937, I, 1–17.

———. 1938. The Movements of Salmon Marked in the Sea. II. The West Coast of Sutherland in 1937. *Fish. Scot. Salmon Fish.*, 1938, I, 1–9.

White, H. C. 1936. The Homing of Salmon in Apple River, N. S. *J. Biol. Bd. Can.*, 2: 391–400.

LOCAL POPULATIONS AND MIGRATION IN RELATION TO THE CONSERVATION OF PACIFIC SALMON IN THE WESTERN STATES AND ALASKA*

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THE study of the migrations of the salmon of Alaska and the Pacific states has been actuated by the conviction that a knowledge of the movements of these fish is essential to the formation of a sound conservation program. The conservation of any species may be defined as the maintenance of the abundance of that species at a level that, with due regard for the requirements of the future, appears to be the most desirable from the point of view of Man. Such maintenance of a population, whether of mice or men or of fishes, requires that the births and deaths shall be equal over a period of time. It is the function of conservation efforts to produce this condition and it is the function of conservation research to provide the information necessary to guide these efforts.

The requirements of practical conservation demand a knowledge of the fluctuations in the birth and death rates and of the events and forces that may cause fluctuations in the birth-death ratio. But any study of the factors affecting the birth-death ratio must take into consideration (1) the extent to which the species is broken up into self-sustaining groups; (2) the fluctuations in the birth-death ratio of each independent group at each stage in the life-history; and (3) the causes of these fluctuations, again for each independent group and for each life phase because these causes need not be and often are not the same for all of the population groups that go to make up the species.

In the conservation of any natural, biological resource it may, I believe, be considered self-evident that the population must be the unit to be treated. By population I mean an effectively isolated, self-perpetuating group of organisms of the same species regardless of whether they may or may not display distinguishing characters and regardless of whether these distinguishing characters, if present, be genetic or environmental in origin. Given a species that is broken up into a number of such isolated groups or populations, it is obvious that the conservation of the species as a whole resolves into the conservation of every one of the component groups; that the success of efforts to conserve the species will depend, not only upon the results attained with any one population, but upon the fraction of the total number of individuals in the species that is contained within the populations affected by the conservation measures. On the other hand, the conservation of a species that is not so broken up into isolated, self-perpetuating groups obviously presents entirely different problems, simpler in some ways, more difficult in others. More general conservation measures may be effective for such species. These population groups have commonly been termed by biologists on the Pacific coast "races," entirely without any implication that the groups show demonstrable and heritable differences. It is true that, in certain instances, the population groups do show demonstrable and heritable differences but it is also true that in many other cases no such differences have been shown. The latter is not surprising in view of the fact that there are certainly scores or hundreds of such population groups in each of the five species of the genus *Oncorhynchus*.

It is apparent then that one of the first requirements of a sound conservation pro-

* Contribution No. 1, Department of Research, Fish Commission of Oregon.

gram must be the determination of the extent to which the species to be conserved is broken up into local populations. The defining of specific populations is concerned to a considerable extent with the determination of the geographical limits occupied by each. This is relatively simple in the case of plants and of other fixed or non-migratory organisms but may prove to be a problem of great intricacy in the case of migratory animals especially such animals as fish which cannot readily be observed directly. Proof of the existence of local populations of migratory species does not, however, depend necessarily upon a knowledge of the extent, direction and duration of the migrations in question; adequate proof may be given by entirely different evidence.

A knowledge of the extent, direction and duration of the migrations is, however, essential to the determination and understanding of the events and forces that affect the birth-death ratio and, therefore, to a sound conservation program. As specific examples the fact that Columbia River Chinook salmon are to be found off the coasts of southeastern Alaska and British Columbia during their oceanic migrations is of the greatest importance to an understanding of the causes affecting the abundance of these fish. It is of importance because, in these northern waters, the fish are subjected to an intensive fishery carried on by hook and line in the ocean and the development of this fishery has undoubtedly increased the rate of mortality although a measure of the effect has not, and perhaps cannot be secured.

Similarly the fact that the red-salmon fishery in the Ikatan-Shumagin Islands district south of the Alaska Peninsula draws almost exclusively upon the runs to Bristol Bay is important to an understanding of the forces affecting abundance and to the outlining of effective conservation measures.

Only through a knowledge of the migrations of these fish could we know the drain that such distant fisheries make on the particular runs.

In general it is obviously important to discover causes of fluctuations in the birth-death ratio. Such causes and their influence on the population may be exceedingly difficult to determine and measure under the best of circumstances, but it is certainly impossible without a knowledge of the movements of migratory animals such as the salmon.

There has been some confusion of these two problems—that is to say, the problem of the existence of local populations and the problem of the nature of the migrations. This is perhaps due to the fact that information on both is so essential to practical conservation and because any complete study of migrations must be preceded or accompanied by a determination of whether local populations exist or not. But in our consideration of the problems relating to the migrations and conservation of salmon it is important that we keep clearly in mind the distinction between the two. A knowledge of both is important to sound conservation, but there is this distinction: While, as I have already pointed out, the demonstration of the existence of distinct populations does not depend on a knowledge of the migrations, a study of the movements of fish requires a knowledge of the population groups to which the fish belong.

Turning now to a consideration of the salmon of the Pacific states and Alaska, I shall take up first the evidence relating to the existence of local populations and then that bearing on the nature of the movements of certain of these populations.

Evidence of the existence of local populations of Pacific salmon may be considered under three heads: (1) morphological and chemical, (2) statistical and (3) experimental.

1. A list of demonstrated morphological and chemical differences between fish running into different streams would be long and varied. It can only be stated here that there have been shown to be constant differences in size, both with and without differences in age; significant differences have been observed in the size of the mature eggs; differences in chemical composition especially as regards the oil content of the flesh have been shown—differences that exist at comparable stages of the spawning migra-

tion and so cannot be ascribed to differences in the length of time elapsed after leaving the feeding grounds; small but statistically significant differences exist in respect of such characters as proportional measurements and counts of vertebrae, fin rays, etc. Of a somewhat different nature are the differences observed in the scale markings which, in effect, provide a permanent and continuous record of the rate of growth throughout the life of the fish.

2. What I have chosen to call the statistical evidences of local populations include the persistence over long periods of time of distinctive age group ratios (as determined from scale examinations) and of distinctive cycles of abundance. The two are often related especially in cases, as that of the famous Fraser River sockeye run, in which the size of the breeding population is the chief determinant of future abundance. Such distinctive cycles of abundance have been demonstrated with statistical significance for a number of Alaskan streams and for at least two species, the red and pink salmon (*O. nerka* and *O. gorbuscha*).

3. Experimental evidence of local populations of Pacific salmon rests chiefly upon the results of numerous large marking experiments involving an aggregate of some three or four million young salmon. These have been marked by clipping fins before or during the seaward migration and the adults were recovered from the commercial fisheries or from the spawning areas. I started a series of such experiments on the Columbia River in 1916 and since then hardly a year has passed in which additional experiments have not been started. Most of these have had to do with the Chinook salmon (*O. tschawytscha*) and the sockeye or blueback (*O. nerka*). The results have shown beyond any reasonable doubt that the marked fish return in overwhelming proportions to the stream and even to the tributary in which they spent the early part of their existence. Aside from the evidence indicating the return of the adults to their home streams these experiments have provided evidence on a number of other problems that do not bear so directly upon the main subject of this discussion. Other evidence, experimental in nature, is that provided by the establishment of salmon runs in streams where no runs previously existed; as in the case of the Chinook salmon run into Spring Creek and that of the red salmon runs that were maintained for a number of years in Herman and Tanner Creeks, all in the Columbia River basin; similarly the gradual rehabilitation of depleted runs when properly protected over a period of years. The mere fact that the run of one stream may be depleted by too intensive exploitation while that of a neighboring stream is not is strong evidence in favor of the existence of local populations. Such a case is presented by the maintenance of a good run of red salmon into the Karluk River on Kodiak Island while the runs into Red River, Uganik River and Little River were being depleted to the point of commercial exhaustion.

To summarize: Diverse evidence points so clearly to the existence of local, self-perpetuating populations in the Pacific salmon that any hypotheses that do not conform must be subject to considerable doubt. This, I believe, must be accepted as a proved fact regardless of what may or may not be discovered about the extent of the oceanic migrations, regardless of how the migrations and particularly the return to the home stream may be accomplished and regardless of the reasons why the movements are made. Practical conservation measures must be based upon the acceptance of the "home stream theory" as an essentially correct statement.

Turning now to consider the nature and extent of the migrations: The general features of the migrations of the Pacific salmons are well known and are summarized in the mere statement that these are anadromous fishes. The details of the seaward migration as to time, rate of travel, age of the fish and so on, have been, and still are, under investigation but are not of particular concern at this time. The details of the oceanic migrations, however, are of major importance both on account of their bearing on certain interesting problems in animal

behavior and on account of their great importance in practical conservation of the salmon fisheries.

There have been two opposing theories: First that the fish, on entering the ocean remain throughout their lives at sea close to the mouth of their home stream—perhaps spreading fanwise but always within the influence of the home-stream water. This was a theory at one time advanced by Dr. David Starr Jordan. The second theory states, in effect, that the fish range widely, far beyond any conceivable influence of the home stream to which, however, they predominantly return.

It was not until an extensive series of experiments involving the tagging of Pacific salmon was started in 1922 that satisfactory data began to accumulate bearing on this question. In these experiments fish were taken with as little injury as possible, usually from traps of the commercial fishery, tagged with standard, serially numbered stock tags and released. On recapture the fishermen were asked to report the tag to the fishery officials with information as to where and when taken. In 1922 and 1923 the late Dr. C. H. Gilbert and myself tagged 14,000 salmon, chiefly reds (*O. nerka*) along the western portion of the Alaska Peninsula from the Shumagin Islands in the south to the region of Port Moller on the north.

When the experiments were begun it was supposed that the fish taken in this region were bound for local streams, although no important local spawning grounds were known. The results, however, showed conclusively that the red salmon were a part of the important runs that spawned in the rivers of the Bristol Bay region over 300 miles to the north and east of the narrow, shallow passage between the peninsula and the first of the Aleutian Islands and 400 miles from Unimak Pass between the first and second of the islands and the first broad, open passage from the north Pacific to the Bering Sea. Later statistical analysis showed a high correlation between the catches of red salmon at Ikatan and in Bristol Bay for the years 1913 to 1925 inclusive. The coefficient of correlation (r) was $+0.79$ —a value that would not occur as a result of "sampling error" alone once in a hundred times.

Incidentally it is this run of red salmon that the Japanese have begun to exploit by gill-net fishing in the open sea along the route of migration between the passes of the Aleutian Islands and Bristol Bay. The importance of a knowledge of the movements of fish in the ocean is well shown in this case in which the results of the tagging experiments of 1922 and 1923 showed clearly the danger to the fisheries of Bristol Bay and the Ikatan-Shumagin Island districts of an additional and unrestricted drain on the natural resources such as would most certainly result from the development by the Japanese of a pelagic salmon fishery in this district. .

Another series of tagging experiments has shown that many of the Chinook salmon taken by the troll fishery off the coasts of southeastern Alaska and British Columbia eventually enter the Columbia River to spawn. More of the tagged fish in these experiments were taken in the Columbia River than in all other streams together and the Columbia is from 300 to 800 miles southeast of the points of tagging.

The question arises as to whether we can assume that the fish that travel these long distances in the ocean are actually returning to their home streams from the oceanic feeding grounds. I believe that this can be answered in the affirmative on the basis of the following argument:

(1) The return of the adult fish, predominantly, to their home streams may be accepted as proved beyond any reasonable doubt.

(2) It is also known that large numbers of Chinook salmon that eventually enter the Columbia River and large numbers of red salmon that eventually enter the streams of Bristol Bay are to be found at sea great distances from the mouths of the streams that they enter.

(3) The only simple theory that can possibly reconcile these two facts is that the fish of the Columbia and of Bristol Bay do return to their home streams even when they

have gone such great distances at sea that they would seem to be beyond any possible hydrographic influence that their home streams might have. If this is true of the Columbia River Chinooks and the Bristol Bay red salmon it seems reasonably certain that it is a pattern of behavior generally common to the Pacific salmon.

As a matter of practical conservation it is obviously of importance to the troll fishermen of southeastern Alaska and of British Columbia that the Columbia River Chinook salmon runs be conserved; and it is of importance to those who are interested in the conservation of the Columbia River salmon to know what is happening on the distant fishing grounds lest the developments there negative the influence of any conservation measures that may be effected in the Columbia River itself. Not that, at present, anything is likely to be done about it; but perhaps, in the fullness of time, some wise legislator will decide that something ought to be done. If that should happen he will likely turn to some biologist and expect an immediate answer to his question as to what ought to be done. Which reflection, however, is beside the point.

My primary interest in this subject is, obviously, that of the practical fishery conservationist, and I suppose that I am inclined to be somewhat impatient with theories and attitudes that I fear may provide ammunition to those opposed, for one reason or another, to true conservation. The entire program for the conservation of the salmon of the Pacific coast and Alaska, so far as it depends from scientific information and not from political exigencies, is based upon the acceptance of the "home stream theory"—in other words, of the theory that the several species each consists of a large number of independent local populations or races and that the adults return from the ocean predominantly to the streams of their nativity. I feel that this theory is on solid ground and must be accepted as fundamental. The practical conservationist must assume, in the absence of any conflicting evidence, that the Pacific salmon do return to their home streams from whatever distance they may go at sea; he must determine the drain upon the salmon runs by fisheries at such distant points as may prove to be in the path of the migration and he must apply his conservation measures throughout the range of the populations in question to the end that each may be maintained at the most productive level.

Summary

1. A rational conservation program for such migratory fishes as the salmon must be based on a knowledge of (a) whether or not the species consists of local, self-perpetuating populations and (b) the nature and extent of the oceanic migrations.

2. The conservation of a species that is broken up into local self-perpetuating populations involves the determination of the causes of mortality at all stages in the life-history of each group.

3. Species that are not so broken up may be conserved by measures of more general application.

4. In the case of migrating species the routes traversed by the individuals of each population group must be known in order that the causes of mortality may be determined and that appropriate conservation measures may be applied.

5. In the case of the Pacific salmon, the evidence shows clearly the existence of local, self-perpetuating populations.

6. The evidence also shows clearly that the Pacific salmon return from their life in the sea predominantly to their home streams thus justifying acceptance of what is known as the "home stream theory."

7. It has also been shown that many of the Pacific salmon travel hundreds of miles in the ocean, by the nearest route, from places where they have been captured and tagged, before they enter streams for the purpose of spawning.

8. In the absence of any conflicting evidence it is believed that the "home stream theory" applies to these fish that travel long distances in the ocean as well as to those that may not travel so far and that the basing of practical conservation measures upon an ac-

ceptance of the "home stream theory" as of general application is justified.

References Cited

Clemens, W. A. 1937. Contributions to the Life-history of the Sockeye Salmon. No. 23. Ann. Rept. Provincial Fisheries Dept. British Columbia for 1937. 1929. Summary of the Results of Tagging of Spring Salmon Along West Coast Vancouver Island and Queen Charlotte Islands in 1925, 1926 and 1927. *Prog. Repts. Pac. Biol. Sta. Biol. Bd. Canada,* No. 4, 11–13.

Clemens, W. A., and Clemens, Lucy S. 1925 to 1936. Contributions to the Life-history of the Sockeye Salmon. Nos. 11 to 22. *Ann. Repts. Fish. Dept. B. C.,* 1925 to 1936.

Davidson, F. A. 1934. The Homing Instinct and Age at Maturity of Pink Salmon (*Oncorhynchus gorbuscha*). *Bull. U. S. Bur. Fish.,* No. 15, 27–39.

Dill, D. B. 1925. The Proximate Composition of Certain Pacific Coast Fishes. *Ind. and Eng. Chem.,* 17: 6, 629.

Gilbert, C. H. 1913. Age at Maturity of the Pacific Coast Salmon of the Genus Oncorhynchus. *Bull. U. S. Bur. Fish.,* 32: 1–22.

———. 1914 to 1925. Contributions to the Life-history of the Sockeye Salmon. Nos. 1 to 10. *Ann. Repts. Fish. Dept. B. C.*

———. 1923. Experiment in Tagging Adult Red Salmon, Alaska Peninsular Fisheries Reservation, Summer of 1922. *Bull. U. S. Bur. Fish.,* 39: 39–50.

Gilbert, C. H., and Rich, W. H. 1925. Second Experiment in Tagging Adult Red Salmon, Alaska Peninsula Fisheries Reservation, Summer of 1923. *Bull. U. S. Bur. Fish.,* 42: 27–75.

———. 1927. Investigations Concerning the Red Salmon Runs to the Karluk River, Alaska. *Bull. U. S. Bur. Fish.,* 43: 1–69.

Pritchard, A. L. 1931. Summary of the Results of Tagging of Spring Salmon in 1929 and 1930. *Prog. Repts. Pac. Biol. Sta. Biol. Bd. Can.,* No. 8, 15–20.

Rich, W. H., and Ball, E. D. 1928, 1931, 1932 and 1933. Statistical Review of the Alaska Salmon Fisheries. Parts 1 to 4. *Bull. U. S. Bur. Fish.,* 44: 41–95; 46: 643–712; *Bull.* No. 7, 187–247, and *Bull.* 13, 437–673.

Rich, W. H., and Holmes, Harlan B. 1929. Experiments in Marking Young Chinook Salmon on the Columbia River, 1916 to 1927. *Bull. U. S. Bur. Fish.,* 44: 214–264.

THE MIGRATION OF PACIFIC SALMON IN BRITISH COLUMBIA WATERS

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MIGRATIONS of salmon have been investigated extensively in British Columbia over a period of 12 years by the Fisheries Research Board of Canada. Two procedures have been followed, namely, tagging of adults for the purpose of determining the movements of the fish in the sea, and marking of young to indicate the extent of return to the natal stream. With the exception of one preliminary experiment pertaining to the function of the olfactory nerves, no attempt was made to determine the causative factors involved in the movement of the fish.

METHODS

In the tagging programs, the majority of the fish were obtained from the commercial fishermen operating the usual types of gear (troll, purse seine and trap) in the various fishing areas along the coast. In a few instances expert troll fishermen were employed to catch spring and coho salmon solely for tagging purposes. A serially numbered aluminum strap tag was affixed to the dorsal portion of the caudal peduncle with a special pair of pliers. A reward of 50 cents was offered for the return of a tag together with information concerning date and place of recapture. Thus the histories of individual fish could be determined.

In the marking programs, fry, fingerlings and yearling fish were captured at the time of their seaward migration and marked by the removal of two or more fins. Rewards were offered for adult fish bearing such scars. Recoveries were made by fishermen, observers in canneries and employees at weirs on the streams. Because of the distinctive marks, these fish could be identified as belonging to the various experimental groups.

Discussion will be limited to the results of the tagging of spring and sockeye and to the marking of sockeye and pink salmon.

THE MIGRATION OF SPRING SALMON

During the years 1925 to 1930 inclusive, tagging programs were prosecuted at various places on the west coast of Vancouver Island, on the west and north coasts of the Queen Charlotte Islands, in the vicinity of the islands near the mainland shore in northern British Columbia, off the northeastern coast of Vancouver Island and in the Gulf of Georgia. Consideration of the detail of each isolated experiment would only serve to confuse the broader general issues. For that reason one typical experiment is selected as an illustration in this presentation and the rest of the data are briefly summarized.

In May and June, 1925, 1,125 spring salmon captured in the commercial troll fishery off Barkley Sound on the west coast of Vancouver Island were tagged in the manner described. In subsequent years 123, or 11 per cent, were recovered. The distribution of these recoveries was as follows: Barkley Sound, 8; Cape Flattery, 3; Strait of Juan de Fuca (British Columbia waters), 7; Strait of Juan de Fuca (United States waters), 7; Puget and Washington Sounds, 11; Fraser River, 6; Pacific coast of Washington, 2; Columbia River, 74; Pacific coast of Oregon, 2; Sacramento River, 2, and unknown locality, 1.

In spite of the factors which might affect the collection of returns in such an experiment, *e.g.*, the loss of tags, the natural mortality of the fish, the failure to return the tags, the effect of fishing intensity on the collection, etc., three general conclusions are justified.

1. Spring salmon make long and compli-

cated migrations off the coast of British Columbia usually in a south and easterly direction. Especially noteworthy is the recapture of two individuals in the Sacramento River, 800 miles from the point of tagging.

2. This habit of travelling long distances exposes the fish to capture at many points and greatly increases the difficulties involved in measures of regulation. As an illustration, spring salmon tagged off Barkley Sound were taken off Barkley Sound, in the Strait of Juan de Fuca, in Puget and Washington Sounds, off the coasts of Washington, Oregon, and California and in the Columbia River.

3. The migrations are definitely international in aspect. In the case under consideration from tagging in Canadian waters 82 per cent of the returns were from territory of the United States.

When a summary of recoveries for all the tagging programs on the species is set up showing the percentage return for the Fraser River, the Columbia River, Canadian waters and United States waters, exclusive of Alaska, it is evident that as the location of the tagging base becomes more northerly, the returns from the waters of the United States, exclusive of Alaska, become fewer, those from the west coast of Vancouver Island averaging approximately 85 per cent, from the west coast of the Queen Charlotte Islands approximately 66 per cent, and from the north coast of the latter together with Hecate Strait, 53 per cent. Coincident with this change the recaptures in Alaska increase from none for the west coast of Vancouver Island to as high as 4 and 2 per cent for the west and north coasts of the Queen Charlotte Islands, respectively. Such a condition presupposes that the individuals which constitute the commercial spring salmon fishery have come from the north and west and are proceeding toward the south and east.

Consideration of the data with special reference to the time of recapture in relation to the time of tagging is also of interest. Our present knowledge of salmon habits and the location of recoveries in the experiments would definitely indicate that those fish which were recaptured in the year of tagging were closely approaching maturity at the time of tagging, while those taken in each succeeding year represented greater and greater degrees of immaturity at the time the tag was affixed. On this basis the fish from Seal Inlet and other northern areas where a lower percentage return was received in years subsequent to tagging, were more mature than those at Barkley Sound in the south. At North Island on the north coast of the Queen Charlotte Islands an indication of immaturity again appears. This is explicable, as shown later, by the assumption that fish of another river system are involved.

The examination by Dr. C. McC. Mottley of the scales from the fish tagged off Barkley Sound in 1926, and Kyuquot in 1927, and comparison with similar determinations made by Dr. Willis H. Rich for fish off the mouth of the Columbia River in 1925, have led to the assumption that the numbers in the older age groups increase as the location moves northward and westward. Confirmation of this was forthcoming from qualitative observations which indicated a wave of young fish passing northwestward, producing a crest of abundance off Barkley Sound in June and off Kyuquot in August.

The tabulation of the weights of the fish tagged definitely shows that the size increases in the more northerly areas, at least up to Seal Inlet on the west coast of the Queen Charlotte Islands. In the northern areas most of the individuals are in the 30 to 50 lb. group while at Barkley Sound the mode lies in the 10 to 19 lb. group. This is again an indication of increasing age toward the north.

From these pieces of evidence, namely the distribution of the returns from the tagging programs with the decreasing numbers from southern rivers for northern tagging bases, the increase of maturity toward the north, a similar increase in weight and age, and the results of marking programs by Dr. Rich and Mr. H. B. Holmes on young spring salmon in the Columbia in which they demonstrated that the fish returned to the stream

TABLE I

GROSS SUMMARY OF ALL THE TAGGING PROGRAMS CONDUCTED ON SPRING SALMON ALONG THE BRITISH COLUMBIA COAST

Area of tagging	Year	Number tagged	Per cent return	Percentage of returns			
				Fraser River	Columbia River	Canadian waters	U. S. waters, exclusive of Alaska
North coast, Queen Charlotte Islands	1929	445	14.2	30.2	23.8	47.7	49.2
" "	1930	662	14.7	16.5	27.8	39.3	57.7
Hecate Strait	1930	182	8.2	6.7	40.0	40.1	53.4
West coast, Queen Charlotte Islands	1925	274	13.5	10.8	27.0	29.7	70.3
" "	1929	375	10.9	17.1	17.1	44.0	56.0
" "	1930	179	13.4	16.7	41.6	25.1	70.8
Milbank and Fitzhugh sounds	1930	302	5.3	25.0	12.5	87.5	12.5
Vancouver Island Hardy Bay	1930	436	6.4	.....	14.3	28.5	71.5
Quatsino Sound	1927	54	14.8	.....	50.0	12.5	87.5
Kyuquot Sound	1927	517	15.5	1.3	60.0	7.5	90.0
Barkley Sound	1925	1,125	10.9	4.9	60.2	17.1	82.1
" "	1926	1,353	13.5	6.6	59.6	16.4	81.4

TABLE II

RETURNS OF SPRING SALMON WITH SPECIAL REFERENCE TO THE TIME OF RECAPTURE AS COMPARED WITH THE TIME OF TAGGING

Area of tagging	Year	Number tagged	Number returned	Per cent return	Percentage of return			
					1st	2nd	3rd	4th
North coast, Queen Charlotte Islands North Island	1929	403	63	15	84	14	2	0
" "	1930	472	67	14	93	7	0	0
Hecate Strait	1930	182	15	8	87	13	0	0
West coast, Queen Charlotte Islands La Perouse Rock	1929	177	20	11	100	0	0	0
Seal Inlet	1929	188	19	10	84	16	0	0
" "	1930	115	16	14	87	13	0	0
Milbank and Fitzhugh sounds	1930	302	16	5	100	0	0	0
Vancouver Island Hardy Bay	1930	436	28	6	93	0	7	0
Quatsino Sound	1927	54	8	15	88	12	0	0
Kyuquot Sound	1927	517	80	16	86	11	0	3
Barkley Sound	1925	1,125	123	11	61	35	3	1
" "	1926	1,353	183	14	77	18	4	1

in which they were hatched, a more or less cohesive picture of spring salmon migration has been set up.

The young from the southern coastal rivers disperse northward along the coast of British Columbia at a slow rate, growing in size and increasing in age. At some time in their life history, these salmon, influenced by an undetermined factor, strike in from the northwest and return southward. From this migration the runs to the many spawning areas break away through the various channels which lead to the different rivers.

The fact that this species chooses mainly the larger rivers in which to spawn must be recognized. The runs from these large

streams will dominate the fishery throughout the areas in which they are travelling but this domination may be masked to some extent by the runs to smaller coastwise areas. It would appear that those salmon which leave the southern rivers do not travel as far north as those from the northern streams before they turn back. Such being the case, the Columbia River's contribution to the fishery would be diminishing as we went north while that for the Fraser River would appear to be increasing. In other words, the area in which a run from any large river dominates the fishery has a northern limit. Such a condition is indicated in the vicinity of the northern Queen Charlotte Islands where the number of fish from the Columbia appears to have become less and those from the Fraser greater. It is only to be expected that what might be termed inshore tagging would result in a less extensive and more local distribution of migrants.

Such is the general picture as portrayed by tagging operations and related data. Further work may clarify many of the features and may lead to the discovery of the causes for certain reactions. It is not probable, however, that the idea of a general northwesterly migration of young fish and the southeasterly return based to a large extent on circumstantial evidence, will be materially altered.

The Migration of Sockeye Salmon

Before dealing with the more recent tagging of sockeye salmon, mention should be made of the first experiment with this species in British Columbia. In 1918, Dr. Rich and Dr. C. MacLean Fraser tagged 831 fish at the traps near Sooke. The results published by Dr. Rich and Mr. Henry O'Malley showed a definite migration route eastward through the Strait of Juan de Fuca to the Washington coast, thence northward through Rosario Strait, past Boundary Bay and Point Roberts to the Fraser River.

In 1925, 519 sockeye were tagged at Deep Water Bay, on Johnstone Strait. Omitting the fish recaptured at the point of tagging, 83 per cent of the returns were from the Fraser River, and another 8 per cent from near the mouth of the river. A definite migration route from the northwest through Johnstone Strait to the Fraser River was thus demonstrated.

Among the 519 fish, 259 had the olfactory nerves severed before liberation. Of these 42 fish or 16 per cent were recaptured, of which 33 per cent were taken in the tagging area, 55 per cent in the Fraser River and 12 per cent in other areas. Of the normal fish 65 or 24 per cent were recaptured, 4.5 per cent in the tagging area, 91 per cent in the Fraser River and 4.5 per cent in other areas. Making due allowance for some physiological disturbance resulting from the operation it is evident that the fish were able to make their way to the Fraser River without the use of the olfactory sense organ.

In 1928, 402 sockeye were obtained from traps at Point Roberts, transported in a boat equipped with a live-well and liberated after tagging at various points in the Fraser River from the mouth to Matsqui. Fifty-four tags were returned, of which 12 were taken upstream from, 13 in the vicinity of and 29 downstream from the point of liberation. The figures are not significant in themselves because of the varied relation between the point of release to the fishing area. They do show that movement upstream is not always a steady progression. There are instances of intervals 15, 22 and 30 days between release and recapture in the river. Of fish liberated at the mouth of the river one was recaptured in the trap at Point Roberts five days later, and two others were not recaptured for 36 and 40 days, one at the mouth of the river and the other 15 miles upstream.

Taking advantage of the temporary operation of a trap at Haystack Island near the entrance to Portland Inlet in 1925, 659 sockeye were tagged during the first three weeks of August. Sixty-five per cent of the returns were from the Nass River, 10 per cent from the Skeena River and 20 per cent from Alaskan waters. Of the latter 5 per cent were from nearby areas, but 15 per cent were from distant points to as far as 105 miles. It is interesting to note that 30 per

cent of these fish which were apparently as much subjected to the influence of the Nass River as were the 65 per cent which went to the Nass, proceeded southward to the Skeena River or northward into Alaskan waters.

Marking of Pink Salmon

Marking of pink salmon, *i.e.*, the removal of fins from the young seaward migrants as a means of later identification, has been undertaken in British Columbia primarily to determine directly the age at maturity, and to discover whether the adults return to spawn in the same streams which they left as fry.

The programs may be divided into two categories, viz., those on the natural runs and those on young fish which were the progeny of eggs hatched artificially. The former include the years 1931, 1933 and 1935, when the fry were taken at random from the natural seaward migration in the spring at McClinton Creek, Masset Inlet, marked and allowed to proceed without further interruption. In 1932 and 1936, the fry marked at McClinton Creek were the progeny of eggs transferred to that area from the Tlell River on the east coast of Graham Island. In 1932, some fish were handled at Sweltzer Creek, a secondary tributary of the Fraser, which were the result of eggs taken the year previous at the same place, their hatching and the retention of the resulting fry for some months.

All returns received from the several experiments were in the summer and autumn of the year following the marking. The salmon at that time were mature and ready to spawn. This is taken as conclusive proof that pink salmon mature and return to spawn in the autumn of their second year.

Amongst those experiments on the natural runs at McClinton Creek, that begun during the spring of 1933 was most successful from the point of view of accurate manipulation and number of returns and is here discussed in detail as representative of the others. During the spring, 107,949 fry were marked by the removal of both ventral fins. The recoveries, all of which were received in the autumn of 1934 were distributed as follows: McClinton Creek, 2,941; Masset Inlet fishing areas, 324; Naden Harbor, 1; West coast of the Queen Charlotte Islands, 3; Ogden Channel, 1; Whale Channel, 4; Bear River, Johnstone Strait, 1, and Deep Bay, 1.

The recovery in McClinton Creek, the "parent" stream, of 2,941 or 90 per cent of the total recaptured, indicates a strong tendency on the part of the pink salmon to return for spawning to the stream in which they were hatched. In addition, the 324 marked fish taken in the fishing areas in Masset Inlet, the one from Naden Harbor, and the three from the west coast of the Queen Charlotte Islands, might also have reached McClinton if they had not been captured by the fishery. The seven remaining recoveries (one from Ogden Channel, four from Whale Channel and one each from Bear River and Deep Bay) were made so late in the season and in localities so far from the original river that it is unlikely that they could have returned there to spawn. The only possible conclusion from such returns is that the majority of pink salmon in the natural runs will return for spawning to the river in which they were hatched. Isolated individuals may "wander" even to a distance of over 400 miles as in the case of the migration from McClinton Creek to Deep Bay on the Strait of Georgia, but the number so behaving is economically insignificant.

The recoveries from those experiments in which fry from transplantation experiments or artificial hatching were concerned, did not prove as consistent in respect to return to the parent stream. From the Tlell fry marked at McClinton Creek in 1932, 40 only were recaptured in the Fraser River fishery. From the 1936 trial, four marked fish returned to McClinton in 1937. The recoveries from the Vedder River marking were located in the Fraser River fishery but no marked individuals were taken at the fences in the Sweltzer itself. It may be that the artificial hatching and consequent transfer of the progeny had an effect upon their later behavior. There are, however, no definite data available at present to support or disprove such an assumption.

Marking of Sockeye Salmon

For sockeye salmon a comprehensive study of the migration, in so far as it pertained to the *return* from the sea, of a population native to Cultus Lake, British Columbia, was made in the years 1930 to 1934.

In the spring months of 1930 and 1931 all the seaward-migrating sockeye leaving the lake were marked. In 1930, 104,061 were so treated by having the two pelvic fins removed; in 1931, from all of the 365,265 individuals migrating the two pelvics and the adipose were amputated. These fish were then liberated to pass on downstream and eventually to the sea.

Returns from the 1930 marking were expected in 1931, 1932 and 1933 as three, four and five-year-old fish respectively, while recoveries of the 1931 group were anticipated in 1932, 1933 and 1934. Accordingly, in these several years arrangements were made to have all or the greater portion of the sockeye landed at the various canneries throughout the fishing areas of the State of Washington and British Columbia closely examined for fish with missing fins. Observers were employed at the necessary points for this sole purpose. During the same years the records of marked fish returning to the parent spawning ground, Cultus Lake, were kept and, in addition, requests were issued to fisheries officers and others throughout the Fraser River system to keep close watch for the presence of marked sockeye among the spawning populations of other areas.

From the fishing areas came very significant returns. Commencing with the purse-seine fishery on Swiftsure Banks, off the entrance to the Strait of Juan de Fuca, the first point adjacent to the open ocean at which migrating adult sockeye are caught, and continuing on in through the Strait of Juan de Fuca, the waters of the San Juan Archipelago, Rosario Strait, the lower end of the Strait of Georgia, to the Fraser River, marked sockeye in all the years in question were recovered. The numbers of marked individuals obtained in 1932 and 1933, arranged according to date and area of capture, are shown in the accompanying table.

TABLE III

Recaptured Individuals, 1932 and 1933

	Swiftsure Banks	Sooke Traps	Salmon Banks	San Juan	Point Roberts	Fraser River
			1932			
Week ending:						
July 30	12	.....	4	1	1	.....
Aug. 6	19	2	46	25	44	.....
13	.....	18	42	25	46	.....
20	.....	48	124	89	39	18
27	2	55	43	57	117	52
Sept. 3	.....	58	39	102	36	70
10	.....	13	.....	16	6	88
17	.....	1	.....	.....	.....	129
24	.....	1	.....	.....	.....	244
Oct. 1	.....	.....	.....	.....	.....	166
8	.....	.....	.....	.....	.....	26
15	.....	.....	.....	.....	.....	3
22	.....	.....	.....	.....	.....	1
29	.....	.....	.....	.....	.....	2
Nov. 1–30	.....	.....	.....	.....	.....	20
	33	196	298	315	289	819
			1933			
Week ending:						
July 17	.....	1	5	.....	1	.....
23	.....	3	1	.....	0	3
30	2	3	11	.....	0	0
Aug. 6	27	2	9	13	6	2
13	135	14	73	104	23	10
20	168	122	477	302	119	23
27	115	179	514	499	468	34
Sept. 3	768	101	938	347	35	84
10	.....	177	900	163	256	255
17	.....	20	64	.....	32	319
24	.....	18	0	.....	27	169
Oct. 1	.....	9	7	.....	5	288
8	.....	.....	10	.....	.....	160
15	.....	.....	.....	.....	.....	96
22	.....	.....	.....	.....	.....	129
29	.....	.....	.....	.....	.....	55
Nov. 1–30	.....	.....	.....	.....	.....	46
	1215	649	3009	1428	972	1673

The trend of migration of the Cultus Lake sockeye seems, accordingly, well defined. Passing seaward from the lake, at an age of one year from hatch, the young fish enter the ocean and presumably proceed off Vancouver Island to the west or northwestward. There they remain from one to three years —the majority return after two—when, with advancing maturity, they commence their return journey. There can be no question of their lingering during the ocean period of residence in coastal or gulf waters for in such case they would be picked up in

the fishing gear at other times of the year or at the same time but in various immature stages. They are encountered first at Swiftsure Banks, the outermost fishing ground for purse-seining, and thereafter are taken throughout the fishing areas.

Proceeding to the parent river, the Fraser, they migrate upstream approximately 70 miles and enter a tributary, the Vedder River, into which, eight to 10 miles above, the parent tributary from Cultus Lake flows. Into this latter they turn and at length reach the lake. Although as close watch for marked sockeye as facilities permitted was made in other spawning areas of the Fraser River system, no record of such occurring was obtained. It would seem, then, that the return of these fish was closely confined to Cultus Lake.

Evidence to support the lack of wandering of sockeye is indicated by the fact that in the two years, 1932 and 1933, when two of the age-groups, three and four, four and five, respectively, consisted of marked individuals, but very few unmarked fish were taken, except those of the age-group which had not been marked. These few might readily be accounted for as individuals which had escaped marking or had been spawned and reared in the stream below the weir. If wandering of returning adult sockeye were general, if no parent stream tendency prevailed, the occurrence of a sizable number of unmarked fish of the principal age-group in each of the two years would have been expected.

Discussion

The tagging of spring salmon has shown: (1) that individuals of this species may travel long distances in a southeastward direction along the coast before entering streams to spawn; (2) that there is a larger percentage of younger fish off Barkley Sound than off Kyuquot or Quatsino Sounds, and (3) that a higher percentage of the tagged fish went to the Columbia River from the west coast of Vancouver Island than from the west coast of the Queen Charlotte Islands.

These facts, together with the results of marking seaward migrating young spring salmon on the Columbia River which demonstrated a definite return to the natal streams, have led to the hypothesis that the young salmon on entering the sea from the various rivers along the coast move northwestward for the most part. This movement may be termed a dispersal or feeding migration. With the approach of sexual maturity a reversal in behavior takes place and the fish travel southeastward to spawn in the various streams which presumably are their natal streams. The above hypothesis appears justifiable on the data available until such time as it is possible to substantiate or disprove it by a large-scale marking program followed by an attempt to secure marked fish in the offshore fishing areas and to tag and subsequently recover them in streams.

In the case of sockeye salmon the picture is clearer in some respects and less clear in others. Marking experiments at Cultus Lake have shown a definite return to the natal stream. Tagging in offshore areas has not been possible and hence distribution and movements in these areas are unknown. However there is certain other information available that is pertinent. From the results of the examinations of the scales of approximately 1,000 fish from each of the Fraser, Skeena and Nass Rivers and Rivers Inlet runs over the past 25 years, it is clear that the sockeye populations of these four main river systems tend to maintain their identities. For example, the Nass River sockeye spend two years in fresh water for the most part and this residence is indicated by double central areas on the scales. The average representation of the 5_3 age-class in the Nass River over the above period of time has been 67 per cent. On the Skeena River the 5_3 age-class has averaged only 9 per cent. Since the central area of the scale is laid down during residence in fresh water and not altered during life in the sea, the differences could not be maintained if there were complete interchange between these neighboring populations. The scale characteristics of the Rivers Inlet fish indicate an equally distinct population. Since the movements of sockeye salmon in the coastal waters are still largely unknown, the extent

of intermingling of populations from the various rivers is necessarily also unknown but whatever the situation in this respect may be, the evidence to date indicates a preponderant return to the natal stream.

Information concerning the migrations of pink salmon is in close agreement with that for sockeye. Marking experiments have demonstrated a return to the natal stream for the most part. Some wandering was discovered but the amount so far revealed is insignificant.

As to the factors involved in the dispersal of Pacific salmon from the rivers and the migration to the spawning areas, little is known. It is generally believed that temperature, salinity and current may be important factors. A preliminary experiment in which the olfactory nerves of sockeye salmon were severed did not indicate a significant amount of wandering.

It is only reasonable to expect that fish which remain near the mouths of their natal streams naturally enter them at maturity. On the other hand, the British Columbia data do not lead one to the opposite extreme conclusion, namely, that fish which pass beyond the natal river influence become lost and do not return. Since the results of the tagging of salmon along the British Columbia coast show a southeastward movement for the most part and over long distances in many cases, and since a definite return to the natal stream has been demonstrated, it may be logically concluded that there is a northwestward movement of the young fish. That these young fish may pass far beyond the influence of the natal stream seems certain. That they return to the natal stream seems equally certain. What physiological changes associated with the approach of sexual maturity and what cyclic changes in oceanographic conditions combine to bring about this return are as yet unknown. What sensory or guiding mechanisms lead the Pacific salmon back to their natal streams are undiscovered. Only a few definite facts concerning the gross features of the migrations are now available and only the patient weaving together of the results of detailed and direct investigations will lead to the solution of the problem.

Importance of Knowledge of Migration to Conservation

The tagging programs have indicated certain migration routes for the various species of Pacific salmon. This information has been of value to the administrative officers in the preparation of fishery regulations and it has demonstrated in many cases the need for international cooperation in devising conservation measures.

The marking programs so far have shown very definite returns of marked spring, pink and sockeye salmon to their natal streams. Future investigations may conceivably indicate less stability of return but until such time regulations for the species should be made upon the basis of the distinctness of the populations of the various river systems.

Summary

1. Two methods have been used to trace the migration of salmon in British Columbia. The first is tagging in which a serially-numbered aluminum strap tag is affixed to the caudal peduncle of the fish. This differentiates each individual fish. The second is marking in which fins are removed from fry, fingerlings or yearlings, thus ensuring group identification later.

2. Tagging has shown that spring salmon may travel long distances in a southeasterly direction before entering the streams to spawn. In so doing they may cross international boundaries and are subject to capture at many points. A higher percentage of tagged spring salmon reach the Columbia River from the west coast of Vancouver Island than from the west coast of the Queen Charlotte Islands. These facts together with knowledge of the return of the species to the natal Columbia as demonstrated by marking experiments, seem sufficient circumstantial evidence to suppose a northwesterly feeding migration and a southeasterly spawning journey for the species.

3. Sockeye salmon marking experiments have demonstrated a preponderant return to the natal streams. Examination of large series of scales from the four main river systems have indicated from the scale pat-

tern that the populations tend to maintain their identities.

4. Marking experiments with pink salmon have so far demonstrated an overwhelming return to the natal river with insignificant wandering.

5. The British Columbia results do not lead one to believe that salmon which pass beyond the influence of the parent stream do not necessarily return to it. Tagging has shown that the fish entering a stream on a spawning migration arrive frequently from far distant points. From circumstantial evidence it is assumed that they migrated the opposite way as young and therefore must have gone beyond their stream influence. Nothing is known of the mechanism causing the return.

References Cited

Tagging—Spring Salmon

Clemens, W. A. 1932. Pacific Salmon Migration: The Tagging of the Spring Salmon on the East Coast of Vancouver Island in 1927 and 1928 with Notes on Incidental Tagging of Other Fish. *Biol. Bd. Can., Bull.* XXVII.

Mottley, Chas. McC. 1929. Pacific Salmon Migration: Report on the Study of the Scales of the Spring Salmon, *Oncorhynchus tschawytscha*, Tagged in 1926 and 1927 off the West Coast of Vancouver Island. *Contr. Canad. Biol.*, N. S. 4, No. 30.

Pritchard, Andrew L. 1934. Pacific Salmon Migration: The Tagging of the Spring Salmon in British Columbia in 1929 and 1930. *Biol. Bd. Can., Bull.* XLI.

Williamson, H. Chas. 1927. Pacific Salmon Migration: Report on the Tagging Operations in 1925. *Contr. Canad. Biol.*, N. S. 3, No. 9.

———. 1929. Pacific Salmon Migration: Report on the Tagging Operations of 1926, with Additional Returns from the Operations of 1925. *Contr. Can. Biol.*, N. S. 4, No. 29.

———, and W. A. Clemens. 1932. Pacific Salmon Migration: The Tagging Operations at Quatsino and Kyuquot in 1927, with Additional Returns from the Operations of 1925 and 1926. *Biol. Bd. Can., Bull.* XXVI.

Tagging—Sockeye Salmon

Bolton, Lloyd L. 1930. Sockeye Tagging on the Fraser River, 1928. *Biol. Bd. Can., Bull.* XVI.

Craigie, E. H. 1926. A Preliminary Experiment upon the Relation of the Olfactory Sense to the Migration of the Sockeye Salmon (*Oncorhynchus nerka*, Walbaum). *Trans. Roy. Soc. Can.*, Third Series, Vol. XX, Part 2, Sect. V.

O'Malley, Henry, and Rich, Willis H. 1919. Migration of Adult Sockeye Salmon in Puget Sound and the Fraser River. App. VIII to *Rept. U. S. Comm. Fish.* for 1918. *Doc. U. S. Bur. Fish.*, 873.

Williamson, Chas. H. See Williamson, 1927, above.

Marking—Sockeye Salmon

Foerster, R. E. 1936. The Return from the Sea of Sockeye Salmon (*Oncorhynchus nerka*) with Special Reference to Percentage Survival, Sex Proportions and Progress of Migration. *J. Biol. Bd. Can.*, Vol. III.

———. 1929. A Report on the Return of Sockeye Salmon Marked at Cultus Lake. *Biol. Bd. Can., Prog. Rept. Pac.*, No. 2.

———. 1930. The Return from the Sea in 1929 of Sockeye Salmon Marked at Cultus Lake in 1927. *Biol. Bd. Can., Prog. Rept. Pac.*, No. 5.

Ricker, Wm. E., and Robertson, A. 1935. Observation on the Behavior of Adult Sockeye Salmon During the Spawning Migration. *Can. Field Nat.*, Vol. XLIX, No. 8.

Marking—Pink Salmon

Pritchard, A. L. 1932. The Return of Marked Pink Salmon in 1932. *Biol. Bd. Can., Prog. Rept. Pac.*, No. 15.

———. 1934. The Interpretation of the Recoveries of Marked Pink Salmon in 1933. *Biol. Bd. Can., Prog. Rept. Pac.*, No. 20.

———. 1934. The Recovery of Marked Pink Salmon in 1934. *Biol. Bd. Can., Prog. Rept. Pac.*, No. 22.

———. 1937. The Findings of the British Columbia Pink Salmon Investigation. Part II. Marking Experiments and Natural Propagation. *Biol. Bd. Can., Prog. Rept. Pac.*, No. 34.

———. 1938. The Findings of the British Columbia Pink Salmon Investigation. Part III. Attempts to Build an "Off" Year Run in Masset Inlet. *Biol. Bd. Can., Prog. Rept. Pac.*, No. 35.

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FACTORS CONTROLLING SALMON MIGRATION

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THE following paper represents an effort to summarize the views on the interpretation of the life cycle of the salmon. The main facts in this story were established in North America by the work of Jordan, Evermann and Gilbert, three distinguished American ichthyologists. To their records have been added many observations and surmises by a long list of subsequent students of the problem. There still remain gaps in this record and conspicuous differences in interpretation which call for further investigation and discussion before the final account can be written.

Among the salmon two groups are recognized; the Atlantic and the Pacific, assigned by ichthyologists on the basis of structure to separate genera. Both are anadromous, spending the larger part of life in the sea and when sexual maturity approaches migrating to spawning grounds in fresh water. The young, hatched out in fresh water, descend to the sea and seek out feeding grounds where most of their growth is achieved. The life cycle of the Pacific salmon is completed with a single journey from fresh water to the ocean and a return to fresh water for spawning; at the close of this period the fish dies. On the other hand the Atlantic salmon survives the spawning period, goes back to salt water and later returns one or more times to fresh water to repeat the process of spawning.

My own studies, which have covered the summer migration period during many years, has been devoted chiefly to observations on the activities of Pacific salmon of the species *Oncorhynchus nerka,* the red or sockeye salmon, in fresh water. Here the case is simpler than with the Atlantic salmon since the entire life span embraces only one cycle; it includes only a single journey down stream, a single trip in the sea to the feeding grounds and return to some river, a single vigorous dash up stream, a single reproductive season and then the end of life.

This journey has often been regarded as similar to the movements of migratory birds but the assumption is a false analogy, based on incomplete data. No Pacific salmon survives to repeat any part of the life cycle. Neither experience of its own nor guidance of companions with knowledge acquired from a previous similar trip can determine or influence its responses to the new environmental conditions which the sockeye encounters at every step of the journey. Add to this the further limitation involved in restricting this study to the part of life spent in fresh water and the problem, complex though it still remains, has yet been reduced to lowest terms. One may rightly hope that continued observations on the active, living salmon will afford some clue to the factors that control salmon migration. To avoid the dangers of narrowly limited investigation of any problem, I have seized the opportunity afforded at times to study the sockeye in different and widely separated areas from Oregon to Alaska, and to compare this species with the other types of Pacific salmon and with the Atlantic salmon as I have had chances occasionally to study them also. The real problem lies in the interpretation of the facts assembled.

THE PARENT STREAM THEORY

The migration of the Pacific salmon as ordinarily explained is expressed by Davidson and Christey (1938: 644) as due to "a high degree of homing instinct, *i.e.,* the majority of the adults return to spawn in the streams of their origin." The thesis is

somewhat more precisely stated by Foerster: "The parent stream theory as advanced and substantiated by Gilbert (1914–24), and Fraser (1920) and others requires that each salmon under normal conditions return to the area from which it came and in which it was reared." This "parent stream theory" is phrased within much narrower limits as the "parent tributary theory." The objections to these theories are numerous and serious from the scientific point of view and I desire to call attention to what I consider defects in this interpretation.

First of all the statement is in no sense an explanation. The use of the term "instinct" has long been criticized by students of animal activities and its lack of meaning been so clearly set forth that it is unnecessary here to repeat the arguments advanced in the discussion. Well established evidences show that the supposed return of the salmon is not without its exceptions and further study may be expected to show that specific factors determine the movements of that minority as well as those of the majority of the fish. To overlook the need of finding an explanation of these movements and to content oneself with a blind phrase leads inevitably to misunderstandings and also turns attention away from the study of those environmental influences which are important in work for the conservation of the species as well as essential to the scientific interpretation of the salmon migration.

I maintain unreservedly that the designation "parent stream" leads to misunderstandings that are unfortunate. Some salmon certainly wander into other streams; the degree to which the fish scatter has not yet been determined. The difficulties in the way of exercising control are very great and conclusions reached are often colored at least by the numerous assumptions introduced into the argument. One series of experiments deserve especial consideration because of the larger degree of control over the movements of the fish that was maintained; this is the work done by Foerster at Cultus Lake, British Columbia (Foerster, 1929, etc.). Here the construction of permanent control apparatus installed at the outlet of a small lake and its constant supervision have given precise data on the departure of yearling sockeye and the return of adults. Thus in 1927 the downstream migrants numbered 249,700, of which 91,600 had been marked by excising the pelvic fins. Of these 4,737 returned as adults in 1929 and 1930, among which 3,930 were unmarked and 804 marked. The percentage of return was 0.88 for marked fish and 2.49 for unmarked fish (Foerster, 1934: 352). The discrepancy in the return might have been due to some unfavorable effect of the marking operation or to inwandering of unmarked sockeye from other areas. The young were liberated immediately after marking and were closely observed; neither infection nor increased mortality was shown and the group appeared lively and perfectly normal on comparison with the unmarked group. This clearly favors the second explanation suggested. Foerster noted particularly that no marked sockeyes wandering to other areas had been reported. He stated further "It is felt that such straying . . . is the result of some exceptional circumstance. . . . Only one situation [exists] . . . in which the return of sockeyes to the parent stream may not take place, that is where eggs have been transferred from one spawning area for planting in another." To me these conclusions appear too narrow. Elsewhere Foerster states that this evidence . . . must be accepted with reservations.

When one considers the conditions on the Pacific coast, the great distances involved, the large number of streams sheltering salmon, the hordes of fish swarming in, the widely scattered spawning grounds, the swarms of fishermen with different gear and methods, the confusion and speed of mass production in the canneries, lack of knowledge and often of interest in competing industrial plants endeavoring to secure the maximum catch and finished product in the brief season with frequent interruptions from unfavorable weather conditions, as well as other difficulties, one may well wonder that any marked fish are ever secured from other points than at just such a

controlled situation as is Cultus Lake. Then notice that almost five times as many unmarked fish returned as marked fish, viz., 3,930 to 804; in percentages nearly three times as many, 0.88 per cent of the marked fish that went out as young to 2.49 per cent of the unmarked young. One may fairly ask by what method one is justified in designating the conduct of the large majority as "straying?" Is not the evidence really unfavorable to the view that the movement was due to a "homing instinct" and more naturally related to the view that the migration of the fish is controlled by environmental conditions which in some cases are such as to bring them back to the place in which they began life and in other cases not? It does not seem necessary to consider here a possible third view that the movements are subject to mere chance.

In further analysis of the situation I propose to accept the compromise that return to the parent stream *may* be the rule and to test if possible the extent to which that assumed response is due to some blind instinct or should be more probably the result of environmental control.

Whether the departure from the assumed rule be 10 per cent or 25 per cent or more awaits determination by further accurate studies. The fact that some fish do go astray is important and the degree to which migration is modified is even more so since it is the means by which other runs are strengthened or new runs are established. Very likely it was the method by which originally the species was dispersed. The conditions under which scattering occurs and the factors which direct or limit it are consequently significant.

In the next place, lakes and rivers are not static habitats; changes in stream conditions are often brought about by natural influences and more conspicuously by human interference. When forests are lumbered off or burnt off, temperature levels are modified, stream flow becomes more variable, amount and type of food are altered and thus conditions may become unfavorable at times of migration or spawning. As these difficulties arise it is essential to have some understanding of the environmental factors that modify behavior. Only through such knowledge is it possible to determine the cause of fluctuations in the run, to distinguish between periodic and permanent changes in numbers or to provide for the conservation of the species. Man must seek to add to favorable conditions as well as to correct or limit unfavorable changes. An old resident of Seattle who was a careful, trustworthy observer and had had long and intimate contact with the Puget Sound region told me that in the early days every small stream along the shore north of Seattle was crowded at spawning time with some kind of salmon. Yet we know that now many of these streams, highly altered, carry no salmon. Are we to consider that each of these streams sheltered a population group that was wiped out, and can each be replanted and develop a new run, or are conditions changed so that they no longer "attract" salmon? Only experimentation will decide such questions and certain it is that planting has failed in many cases to establish new runs in some of these streams.

In numerous lakes both in America and in Europe are found landlocked races of different salmon. Their close relationship to sea-run species is generally recognized. In another paper (Ward, 1932) I have discussed these groups and have shown that they are not shut off from the sea by impassable material barriers, but that they are probably held back from migrating to salt water by temperature conditions which limit their movements. This view is supported by the discovery of a newly formed race which was cut off from its former pathway by temperature changes incident to the building of a high dam and the consequent formation of a stratum of warm water in the course of a cold river. Such changes in environmental conditions certainly can alter and have altered the original relations of the salmon to the stream. In this manner originated a landlocked group which was restrained by a permanent change in temperature conditions. Furthermore the temperature may affect variably young sockeyes at different ages and, in connection possibly

with the food supply present in given localities, lead this species to remain in a lake for a variable period. It has been found that very few sockeye fry start immediately for the ocean; but that most of them remain for a time in a lake where some of them stay one year, others two and a few even three years in fresh water as the extensive records of W. A. and L. S. Clemens (1926–1937) show. Such data indicate that variations in environmental conditions modify the activities of salmon within the parent waters. Foerster (1937) gives valuable data on this point.

The evidence which has been secured for the return of salmon to their own native waters in the opinion of some is not more than sufficient to indicate a general compliance with this practice whereas in other minds it constitutes a habit little short of absolute, involving a uniform return to the tributary and even to the particular spawning ground involved. Dismissing accounts by untrained observers, let us examine briefly the evidence for the return obtained by scientific students of the problem. These data deal chiefly with physical facts in two lines, (1) scale markings of the adults and (2) the return of fish marked as young. The array of data in these two fields is large and impressive. It represents an important contribution to the solution of this question and is regarded as conclusive by many who have devoted themselves to these experiments. Nevertheless the data are statistical and mechanical, and necessarily subject to the limitations of all similar data. One is justified in asking how far the results obtained for a few fish may correctly be extended to cover the entire groups involved and whether further evidence from a diverse point of attack may not be needed to establish conclusions so far reaching and so heavily loaded with implications concerning the characteristics of living matter. I have myself felt that more extended field studies on the habits of the salmon and more definitely controlled experiments completely followed up would throw valuable light on the situation. The dangers of extrapolation in biology are well recognized, and after all the fish is a living organism and not to be handled merely as a simple mathematical unit.

Scale Markings

In considering the implicit reliance of some on *scale markings,* we must not overlook certain other facts. It is well known that in the past good investigators have made mistakes in their interpretation of such markings and that markings are not uniform in scales taken from the same population group in different years. While some of these differences have been explained, and perhaps rightly, there still remain details unadjusted and differences of opinion which cannot be overlooked and should not be forgotten. In the hands of some (Clemens and Clemens) the careful discrimination of age groups has yielded most valuable information on the life history and migration of population groups in British Columbia streams. Nevertheless I think it fair to include in the category of doubtful items also the fact that the extent to which such scale markings furnish detailed evidence concerning the origin of population groups has not yet been fully demonstrated.

Some able investigators who have devoted much time and care to the study of scale markings are convinced that they furnish thoroughly dependable means of determining not only the age of a salmon and the varied experiences during life but also the precise region from which it came. The latter depends on minute characteristics which, according to their studies, are shared by scales from fish belonging to a particular spawning ground, like individual finger prints, and are not found in scales of salmon from any other region. This was the view of Gilbert regarding salmon from the Fraser River region in which are numerous spawning areas and it implies great if not absolute fixity of populations in these areas. If this view be accepted, it is at once apparent that no appreciable addition can be made to the population of an area from any other region, since, if foreign adults should creep in, the scale markings would become

modified in some of the hybrids and even small intermixtures in the course of a few years would result in general confusion of the group pattern. This is clearly shown by the work of Foerster in his studies on the scale markings of Cultus Lake sockeyes (1936). He demonstrated variability in scale ring counts in a single season; and also changes in counts from year to year in the same area. These make extremely doubtful any general separation of regional groups on the basis of scale markings. In consequence, I cannot share the views of those who regard scale markings as adequate and final testimony to the origin of an adult salmon. To me this view appears to be too nearly the revival of the long outmoded idea of the absolute fixity of species or varieties and entirely out of line with well demonstrated facts concerning the variation of types.

Return of Planted Fish to Salmon Streams

In the past many experiments have been tried in the effort to establish new runs of Pacific salmon. Both eggs and fry have been planted in large numbers at various points in the hope to populate streams in which no salmon were previously known or to increase the distribution of salmon in river systems which had valuable runs at specific points but were without salmon in other branches that appeared equally if not more favorable for salmon propagation. A few of these experiments have been successful in a degree but none of them in a large way. On the other hand most of them have been total failures and these include experiments that were large and were carried out by able, energetic and well trained personnel. I wish to discuss here in detail a few of these efforts.

One of the earliest was the effort of Captain Callbreath to establish a private run of red salmon on Etolin Island, Clarence Straits, Alaska. Over a period of some 20 years he hatched and planted in his lake yearly large numbers of sockeyes in the hope of securing returns of value. I believe that not a single adult salmon ever came back to ascend the stream or reached the lake on which his hatchery was located. A series of experiments to extend the range of the natural spawning area in the Skagit River system was carried on by the U. S. Bureau of Fisheries. The run of sockeyes in this river was noted for its quality and unique character as the only run of reds in an American stream on Puget Sound. This run left the Skagit at Concrete, taking at a reentrant angle the Baker River, a large tributary, and going up to Baker Lake where the run had natural spawning grounds. The fish were all caught in a trap at the entrance to the lake, kept under control and the new generation planted in the lake or at other points in the Skagit River system. The fish were known as the Baker River run and have been much studied and discussed by those interested in salmon problems.

Both eggs and fry from this run were planted at various points in the Skagit River system, as well as elsewhere to a smaller extent. While no printed records testify to the results it is believed that of these numerous experiments no new runs have been made; in none of the streams planted were runs of adult reds seen later. All of the experiments were apparently unsuccessful, and in one sense that was certainly correct; they did not result in making red salmon streams of the tributaries in which these young descended to the Skagit nor spawning grounds of the lakes in or near which they were planted. An examination of the map of this region shows that almost all the points selected were located on the Skagit River system above the junction of the Baker River. Accordingly, it is not necessary to conclude that the total number of planted fish perished. Even though circumstances in general may have been adverse, it appears much more likely that some survived and at the appropriate time started from feeding areas in the sea on their migration to spawning grounds. All those which entered the Skagit would in conformity with the environmental influences turn into the Baker River and become part of the Baker Lake spawners.

Great care was exercised in selecting appropriate places and in planting the eggs or fry, but unfortunately the experiments were not followed up sufficiently to determine the results, even at the points where plantings were made. Such experiments are crucial in two diverse respects: (1) Do the fish return to the place at which they were planted, and to what extent? (2) Does any part of the plant return to other tributaries in the river system in which they were planted, and, if so, under what environmental conditions?

My own observations and experiments seem to show that if adult sockeyes return to a stream at all, they return only to certain points in it. Their route is determined by environmental conditions present at the time of their return and that return is controlled not by the geographic location of the point of spawning of adults or planting of young, but by the influence of exciting environmental conditions. In the case of plantings made in the Skagit River above the Baker the fish will return, if at all, not to the upper Skagit and to the tributary in which they were planted, but under present conditions to the Baker River.

Plantings of Salmon in Foreign Waters

Salmon eggs or fry have been at various times planted in waters that had no relation to their ancestral home. Confidence has been generally expressed that the adults would return to the stream or lake in which the plant was made. Records of these experiments are scanty, scattered and incomplete. It looks as if the confidence felt was regarded as adequate evidence of the results. Of unsuccessful plants made in streams that were not known to be salmon waters, I have found no printed records but I have been told of such plants from which no salmon returned.

At one time three million eyed eggs from Yes Bay, Alaska, were brought down, hatched and planted at Baker Lake, Washington. The Yes Bay strain is one of the largest and finest of all sockeyes obtained anywhere on the entire Pacific coast. The plant was made years ago and the strain is said to be recognized even today among the fish caught below the dam on the Baker River. Nothing is more certain than that the route followed and the feeding grounds visited by these fish were entirely foreign to their ancestral record. But the experiment dealt with waters known to support a run of the same type of Pacific salmon.

The results of planting fish in Masset Inlet by Pritchard (1938) have an important bearing on this phase of the problem. Large runs of pink salmon occur in some districts only every second year. Masset Inlet is an extreme example. An effort was made in three "off" years to establish a run. The results are stated thus: "On the basis of the three completed experiments the conclusion is inevitable that the transfer of pink salmon eggs from the Tlell River to McClinton Creek in an effort to build an 'off' year run has been unsuccessful."

Equally striking was the series of experiments conducted by Foerster (1934a: 61–2), summarized as follows: Since the rock slide in 1913 at and above Hell's Gate in the Fraser River, the runs of sockeye salmon to the upper areas of the river system have been very small. For many years efforts have been made to restore the runs by the transplantation of eggs and fry from the lower areas of the river and from the Skeena River. An experiment designed to test the success of such a procedure was undertaken on Eagle River, a tributary of Shuswap Lake. Prior to 1913 Shuswap Lake was one of the most important areas for sockeye salmon propagation and Eagle River one of its most important spawning streams. In the spring of 1929 the Department of Fisheries planted 17,000,000 Cultus Lake eyed eggs in this river and the Biological Board liberated 123,550 marked fingerlings from retaining ponds. In 1932, 17 unmarked sockeye were obtained at the counting fence erected in the river and one marked individual from the experiment of the succeeding year. Fifteen marked fish were captured in commercial nets in the Fraser River. In the late summer of 1930, 271,632 marked fingerlings reared from eggs obtained from the Adams

River, a large tributary of Shuswap Lake, were liberated from rearing ponds at Taft into Eagle River. In 1933, 15 fish appeared at the counting fence of which two were marked individuals. The experiment in the reestablishment of sockeye salmon runs to this river by transplantation has thus met with little success.

Experiments in Marking Young

Marking young salmon has been tried as a means of securing evidence of the return to spawning areas; both fry and fingerlings have been used. One of the first experiments of this kind was that of Chamberlain (1907). He mentions briefly some earlier experiments and describes his own in August 1903, when 1,600 sockeye fry reared at the Fortmann Hatchery from 1,902 eggs were marked by excising both ventrals. They were released in the Naha River just above the hatchery. In 1906 between 50 and 100 adult sockeyes with ventral fins missing were reported by the hatchery superintendent at Yes Lake, which is miles away across the Behm Canal. Only two such fish were obtained at the Fortmann Hatchery in 1906 and seven more were taken there in 1907. "This result is a direct refutation of the homing theory" writes Chamberlain (p. 78). He outlined some other experiments which yielded no positive results. His article contains important data on the biology, life history and differentiation of the species of Pacific salmon. It has not received appropriate recognition from later workers. For reasons not adequately discussed this work has been set aside by later writers as inconclusive.

When I was first on the Naha River in Alaska I was told of this work and attempted to arouse interest in the experiments. It was difficult to do so as every one was thoroughly convinced that the fish would come back, so that the results of the experiment were of no importance.

The method has more recently been widely employed and apparently incidentally tried at some places but not well followed up. I have been told personally of the appearance of such marked fish at points where the observers did not succeed in tracing the fish to any source where experiments in marking young fish were being conducted. Reports of marked fish are subject to various errors and cannot be accepted without careful verification; nevertheless accounts of most experiments betray two defects. First, public records have not been made of all such experiments; second, and more unfortunate, is the fact that little effort has been made to follow up and report in detail the results even of the larger and more significant experiments. Where any reports at all have been published they are confined to a brief statement of the number recovered. I have not found records indicating the extent of the area combed for returns of the experiments. While such records would be imperfect in any event, evidence supporting the home-stream theory has been more assiduously sought than any which might indicate exceptions to it. Of course, any proof of scattering would be at best difficult to secure and imperfect in any case, but those difficulties make the scanty records one might obtain of greater value in testing the theory than the evidence on the other side.

Extensive tests by marking young fish have been made by Rich on spring salmon, by Foerster on sockeye salmon and most recently by Davidson (1934) and Pritchard (1938) on pink salmon. The most extended discussion of experiments in marking young salmon is that given by Rich and Holmes (1929) who reported on work done with chinooks on the Columbia River between 1916 and 1927. They discarded reports of earlier experiments made by Hubbard, Chamberlain and some others as doubtful cases because of imperfect methods. Of more careful experiments which they made the results are summarized thus: "Returns range from one out of 50,000 liberated to one out of 300 liberated; these figures have very little significance, however, because they represent not the total returns but an unknown and varying proportion of the total." One may fairly ask whether the large discrepancy is not of some significance and should have been passed without further analysis. One must bear in mind, to be

sure, that the results given were not obtained by trained observers, for the authors inspected but a small fraction of the run and that at selected points only. Yet further inquiry is appropriate. Are the missing 299 marked fish in the most favorable experiment to be considered as representing the mortality which those salmon suffered during the life in the sea? If so, do not the extra 167 missing in the other unfavorable experiment represent the proportion of that group which went to some other areas? Others have calculated a much larger percentage of returns than the ratio 1:300 established by the most successful record that Rich and Holmes cite; calculations based on those reports would give an even larger number of wanderers than indicated by the marking experiments of Rich and Holmes.

The conclusions reached by Rich and Holmes furnish further interesting items. After stating (p. 262) that the parent-stream theory is "now substantiated by such a wealth of evidence that it seems nearly superfluous to state that none of the salmon marked in the Columbia have been recovered in any other river system" the authors continue: "the tagging experiments in British Columbia in 1925 (Williamson, 1927) show *conclusively* that a large percentage of the spring (chinook) salmon caught by troll in these waters *originated in the Columbia River.*" [Italics mine.] The Williamson article has been carefully scrutinized and gives the following testimony. Under joint auspices extensive tagging of *adult salmon* was carried on off the west coast of Vancouver Island, and off the Queen Charlotte Islands. These fish scattered widely, reaching many different spawning grounds. But at no point in the paper is any evidence furnished to show that the author who was in charge of the operation knew from what streams these fish had come as young or by what route they had reached the points at which they were captured. Accordingly it is difficult to see on what grounds Rich is justified in the statement quoted above. So far as the Williamson article is concerned this comment by Rich is purely an assumption based on the fact that these adults after being tagged were recaptured in the Columbia.

Unquestionably the most safely guarded experiments on marked young salmon were those planned and carried out with great care by Foerster at Cultus Lake, British Columbia. Because the outlet of the lake is completely closed by traps, records could be made of every outgoing fish, fry or yearlings, and of every incoming adult. In a series of papers entitled "An Investigation of the Life History and Propagation of the Sockeye Salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia," and in other separate articles, Foerster and his coworkers have recorded results of fundamental worth. Some items from these reports have already been cited in this paper; here I wish to add further notes on the return of marked salmon.

The work at Cultus Lake started with the spawning season of 1925. The first experiments on marking sockeye migrants were made in 1926 by removing both pelvic fins in 101,200 out of a total run of 1,400,000; these were due to return in the fall of 1928 (Foerster 1929b: 26). In 1927 both pelvics and also the adipose fins were removed from 91,600 out of a total downstream migration of 249,700, both one-year and two-year fish, due to return in 1929. Returns in this class have already been cited in this paper as 0.88 per cent of total marked and 2.49 per cent of unmarked, the discrepancy indicating a probable inwandering of sockeye from other regions.

In reporting the life cycle of the 1926 year class Foerster (1936) recorded that from the group of 1926 migrants both pelvics and half of the dorsal were removed from 99,700 sockeye, or 29.7 per cent of the entire outgoing young of that year. No marked three-year adults returned in 1929 and no marked five-year adults appeared in 1931. In the fall of 1930, adults were taken to the number of 1,340 marked in that manner and this group formed 1.34 per cent of the number operated on. Foerster calculated the return of unmarked adults in this class as 3.2 per cent. While he regarded the data for unmarked adults as subject to sampling

errors, he recognized that this difference between the two groups of marked and unmarked adults, 1.34 and 3.2 per cent was of the same order as that of 0.88 and 2.49 per cent given for the 1927 class. He deferred discussion of this discrepancy until other data could be presented.

In my opinion the figures are indicative of inwandering of adults from other areas and can not be reconciled with the parent-stream theory. The recovery of 341 marked Cultus Lake sockeye from widely scattered fishing areas, twice as many as reported in the previous experiment, is clearly indicative of the scattering of salmon bred in a particular stream and in part at variance with the parent-stream theory as defined by Foerster (see quotation near the beginning of this paper).

In 1932 Foerster and Pritchard (1934: 82) marked pink salmon fingerlings at Cultus Lake. All 8,741 fish marked were liberated in the Vedder River and in 1933, 64 or 0.73 per cent were taken at various points. The captures showed that pink salmon migrate both north and south around Vancouver Island and no marked fish appeared at Cultus Lake among 800 unmarked which "apparently indicates failure to locate the parent stream." This and other "experiments at Masset Inlet seem to indicate that the parent-stream theory may not apply rigidly in the case of the pink salmon." The returns at Masset Inlet indicated a substantial though not complete return to the natal stream. But why do these authors use the word "*rigidly*" when their figures show not one specimen of marked fish of this species taken at Cultus Lake, although the entire run there was caught and examined by trained helpers!

Wandering Fish

While the actual returns of marked fish have been very small in fact, yet the emphasis has been laid by some investigators on the failure to secure more than trivial instances where such fish have been captured at other streams. This argument appears on analysis to have little weight. The area of the field, the number of fishermen and plants involved, the variation in methods of handling the fish captured, the frequent occurrence of other defects in salmon handled, the speed of the cannery processes, and the emphasis laid by canners upon constant care for other details make the chances small that any operator will find any particular defect, even if adequate information has been given to all workers in advance. When these and many other variable and unfavorable conditions are considered, the discovery of any wandering marked adults certainly deserves especial emphasis. Since the chances are so small, these few cases carry far more relative weight than the taking of a much larger number in the home stream where everyone is alive to the exact form of the experiment and interested in the outcome.

The experiments made by marking the fry have been depended on to show that salmon return to the stream in which they were hatched. Data on that part of the problem have already been given and discussed. However one feature of the experiment has received scant attention; that is, the source of the number of unmarked adults returning at the same time. If mentioned at all the figure is usually merely recorded without comment. One exception to this is the report of recent experiments at McClinton Creek, British Columbia. Here Pritchard tabulated for three successive cycles of pink salmon the number of fry migrants and of returning adults for marked and also for unmarked fish. He states "In every cycle the proportionate return of unmarked fish to McClinton is distinctly larger than that for 'marked'!" The most immediate reason for this disparity might be an apparent disadvantage of the maimed young in the struggle for existence. But on the basis of experiments with such marked young held in fresh water for three months, Pritchard rejects the idea that they are handicapped. Yet after brief discussion of the lack of evidence for the basis of this differential mortality, he stated that the data available here are inconclusive.

Tagging Adult Salmon in Salt Water

Experiments in tagging adult salmon at feeding grounds or returning to spawn have been carried out for some years under the auspices of the U. S. Bureau of Fisheries and in Canada. The first were by Williamson, and by others under the direction of Rich. More recently they have been continued by Davidson whose papers include a summary of the earlier work. This work indicates clearly definite lines of movement followed by adults returning from oceanic feeding grounds. They also give some evidence on definite times of migration for different groups of fish. The percentage of tagged fish recovered was large enough, especially in later experiments, to determine both routes and time; they show almost the same definiteness for the migration route as is necessarily involved in fresh water movements. Davidson made in one place the significant observation that with a southeast wind one course is followed in the main but "if a southwest wind is blowing the opposite course is more apt to be taken." Since wind direction certainly modifies locally water movements, Davidson's observations evidently suggest current influence on movements of the salmon.

The work done by Williamson (1927: 305) led him to the following conclusion: "The result of the tagging experiment is encouraging, but as in most similar investigations there is a larger proportion of the tagged fishes of which *no trace has been found.* The sockeye returns are the largest and it is significant that 20 per cent were recaptured in each experiment. Most of these were found *in or in the vicinity* of rivers which they were entering to spawn. But *what of the remaining 80 per cent?*" [Italics mine.] Williamson's query has never been answered and so far as I have been able to find *no intensive* search has been made for the missing 80 per cent. In Davidson's last paper he states that "the majority of the adults return to spawn in the streams of their origin" (1938: 644), but in the tables given in that same paper one may read the following summaries regarding the most successful catches recorded: Recoveries of different dates—At Cape Fox, 26 to 376 fish at one point, total 1,159 fish constituting from 19 per cent of those tagged at one point to 29 per cent of all adults tagged. At Cape Chason 10 to 373 fish recovered at one point in a total of 968 constituting from 23 to 42 per cent of those tagged at one point or only 25 per cent of the total tagged. At McLean Point the total of 998 recovered was highest, forming 41 per cent of all fish tagged. At other points the record shows that lesser percentages of those tagged were recovered later. These figures demonstrate that in Davidson's experiments the proportion missing was smaller than in Williamson's. But *those not accounted for still constitute 60 per cent or more of the numbers tagged.*

These experiments appear to give no significant evidence on the question at issue in the discussion of the parent-stream theory, although often cited to establish its verity. The origin of the salmon tagged was not known, and hence their ultimate destination was not the parent stream except by assumption. Both authors state that only a few tagged fish were recovered on spawning grounds and neither states whether that number was obtained in a single spawning area though Davidson remarks frankly "it is not improbable that salmon occasionally stray from their normal course of migration." The extent and character of that departure from the assumed uniformity is precisely the question at issue. These experiments are of high value in tracing the precise migration routes, and it is to be hoped that they may be continued and extended.

Davidson's paper contains another suggestive finding. His final conclusion reads thus: "Again we find a seasonal difference in distribution. The early migrants are destined for the localities remote from the sea, the later migrants for the more proximate localities." One may well ask whether all the fish in one population group return at the same time to reach under fixed environmental conditions one area in fresh water or whether the fact that environmental con-

ditions in fresh water, changing as has been shown in current, temperature and other factors with advancing seasons, do not condition the return of fish in one month to one region in the stream and in another season to another stream or to a different part of the same stream. Indeed seasonal variation in currents alongshore which are well recognized locally in salt waters, may play an important part in the sorting of fish as found by Davidson and shown in his conclusion just quoted.

Studies on Pacific salmon furnish instances from particular places or years which deserve special mention in this discussion. As an example may be cited the following account from Rich and Ball (1931: 670) on the run of pink salmon at Karluk: "Escapement of pinks [at Karluk] in 1924 was tremendous . . . a conservative estimate . . . in excess of 4,000,000. All entered latter half of July and in August. . . . Decaying bodies so polluted the water that nothing could remain in the stream and survive. . . . Beach for miles covered by remarkable aggregation of salmon bones." This occurrence can apparently not be explained on the basis of a "homing instinct." It may easily be seen as the results of some unexpected shift in local currents or temperature in the sea. Such changes are known and recognized by fishermen as well as by oceanographers.

Evidence of Environmental Control

Long continued observations on the activities of Pacific salmon during the period of fresh water migration has yielded some definite information regarding specific factors which appear to exercise control over the movements of the fish during that period. The situation is far less complex than that offered by the ocean migration, the factors more narrowly limited, less variable and more easily observed and measured while at the same time the fish are more readily seen and followed. Furthermore conditions are in part at least subject to control and modification so that while in fresh water continued observation of small groups is often feasible, some experimentation is also possible, and conclusions may be more readily tested. For these and other reasons I decided to confine my own attention to the fresh water migration and further primarily to that of a single species, the red salmon or sockeye (*Oncorhynchus nerka*). In this way I hoped to avoid confusion incident to combining in a single record activities of separate species which, although manifesting evident relationship, still exhibited constant detailed differences in habit as well as in structure. The results of my studies are contained in papers already published (see literature list at end of this paper) and in others under way. They are not as extensive as one might wish and they have left many questions still unanswered. But in my opinion they have disclosed much which can not be reconciled with the conception that some blind instinct forces the returning adults to follow a predetermined path regardless of the changes that time brings about.

On the Atlantic coast, Huntsman has already shown for *Salmo salar* the influence of environmental factors on the movements of the fish in salt water. Further studies on the Pacific salmon will no doubt add further evidence of environmental control in salt water on species of *Oncorhynchus*. Recent work on oceanic canyons and currents along the north Pacific coast have made extensive discoveries of conditions hitherto unknown which are surely of some import in controlling movements of the Pacific salmon during its marine life.

Summary

While in the main the phases in the life cycle of the salmon have been established, its migration is still unexplained. According to popular view salmon return to the natal stream. The author's studies, purposely limited chiefly to the freshwater period and to the single species (*Oncorhynchus nerka*), thus attacked the problem in its simplest form and have led to questioning the tenability of the home stream assumption. Analysis in detail of the records given by previous investigators revealed gaps in the evidence, exceptions to the rule and conditions unexplained by the simple

assumption; this was coupled with search for control factors which are found in the environment. Specific instances of the influence of mechanical, physical and chemical stimuli were found to be related to particular activities in the life cycle.

There have been reviewed the studies made by previous writers on scale markings, on the return of planted fish and of marked fish, on the wanderings of tagged fish, and other experimental and observational data offered to substantiate the fundamental assumption that control is due to some mystical impulse or inborn instinct. It is found that inadequate attention has been given to the behavior of free living fish under varying conditions. It is important to follow the fate of the large number missing from the records cited rather than to place complete reliance on the small percentage which conforms to the results expected. The aquatic environment is complex even when most narrowly limited as in fresh water, and few only of the many stimuli have been as yet subject to observation or experiment. But, on the basis of studies thus far made on the migration of the salmon, environmental control interprets more fully the data secured than the assumption of blind instinct.

References Cited

Chamberlain, F. M. 1907. Some Observations on Salmon and Trout in Alaska. (U. S. Fish. Com. Rept. for 1906.) *U. S. Bur. Fish., Doc.* 627.

Clemens, W. A. and L. S. 1926–1937. Contributions to the Life History of the Sockeye Salmon. *Repts. Brit. Col. Comm. Fish.*

Davidson, F. A. 1934. The Homing Instinct and Age at Maturity of Pink Salmon (*Oncorhynchus gorbuscha*). *U. S. Bur. Fish., Bull.* 48: 27–39.

———, and Christey, L. S. 1938. The Migration of Pink Salmon (*Oncorhynchus gorbuscha*) in the Clarence and Sumner Straits Regions of Southeastern Alaska. *U. S. Bur. Fish., Bull.* 48: 643–666.

Foerster, R. E. 1929. An Investigation of the Life History and Propagation of the Sockeye Salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia, No. 1. Introduction and the Run of 1925. *Contrib. Canad. Biol.*, N. S. 5: 1–35.

———. 1929a. An Investigation, etc., No. 2. The Run of 1926. *Contrib. Canad. Biol.*, N. S. 5: 37–53.

———. 1929b. An Investigation, etc., No. 3. The Downstream Migration of the Young in 1926 and 1927. *Contrib. Canad. Biol.*, N. S. 5: 83–92.

———. 1934. An Investigation, etc., No. 4. The Life Cycle of the 1925 Year Class with Natural Propagation. *Contrib. Canad. Biol.*, N. S. 8: 347–355.

———. 1934a. Investigations—Transplantation. *Ann. Rpt. for 1933, Biol. Board Can.*, 61–62.

———. 1936. An Investigation, etc., No. 5. The Life History Cycle of the 1926 Year Class with Artificial Propagation. *J. Biol. Bd. Can.*, 2: 311–333.

———. 1937. The Relation of Temperature to the Seaward Migration of Young Sockeye Salmon. *J. Biol. Bd. Can.*, 3: 421–438.

———, and Pritchard, A. L. 1934. Report on the Marking of Pink Salmon Fingerlings at Cultus Lake in 1932. *Ann. Repts for 1933, Biol. Bd. Can.*, 83–84.

Pritchard, A. L. 1938. Transplantation of Pink Salmon (*Oncorhynchus gorbuscha*) into Masset Inlet, B. C., in the Barren Years. *J. Fish. Research Bd. Can.*, 4: 141–150.

Rich, W. H., and Ball, E. M. 1931. Statistical Review of the Alaska Salmon Fisheries. Part II. *U. S. Bur. Fish., Bull.* 46: 643–712.

———, and Holmes, H. B. 1929. Experiments in Marking Young Chinook Salmon on the Columbia River, 1916–1927. *U. S. Bur. Fish., Bull.* 44: 215–264.

Ward, Henry B. 1922. Some of the Factors Controlling the Migration and Spawning of the Alaska Red Salmon. *Ecology*, 2: 161–234.

———. 1930. Some Responses of Sockeye Salmon to Environmental Influence During Fresh-water Migration. *Ann. Mag. Nat. Hist.*, Ser. 10, 6: 18–36.

———. 1932. The Origin of the Land-locked Habit in Salmon. *Proc. Nat. Acad. Sci.*, 18: 569–580.

———. 1938. Environmental Stimuli and Salmon Migration. *Commemorative volume "Grigore Antipa" Imprimeria Nationale*, Bucharest, Roumania, 667–679.

———. 1939. Salmon Psychology. *J. Wash. Acad. Sci.*, 29: 1–14.

Williamson, H. C. 1927. Pacific Salmon Migration: Report on the Tagging Operations in 1925. *Contrib. Canad. Biol.*, N. S. 3: 265–306.

CHEMICAL FACTORS AFFECTING THE MIGRATORY MOVEMENTS OF THE PACIFIC SALMON

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MUCH excellent and necessary work has been done toward the solution of the problem of the migration of the salmon since the beginning of the studies of their migration routes in 1922. The systematic studies of the scales of salmon have added much important information.

Certain of these earlier discussions have approached the subject from the point of view that the salmon returns to the parent stream for the simple reason that it was the stream from which it originated. In recent years some doubt as to so simple an explanation has arisen in certain quarters.

Barnes (1937) in his *Textbook of General Physiology,* page 452, states, "If only a millionth of the time and money lavished on the investigation of endocrines of mammals were spent on further studies of the hormones of invertebrates, we might begin to have some realization of the hidden powers of chemical regulation throughout the living world." The author will accept Barnes' statement and look to the more recent advances in mammalian physiology for physical and chemical receptors, and see how they are applicable to the problem of salmon migration.

In certain places, namely the aortic arch and the carotid sinus, the blood vessels of mammals have receptors sensitive to pressure and to certain chemical substances, such as oxygen and carbon dioxide tensions. This has been shown by various investigators, Cyon and Ludwig (1866) for pressure in the aortic arch, Herring (1924) for pressure in the carotid sinus, J. F. and C. Heymans (1927) for respiratory gases in the aortic arch, Heymans and Bouckaert (1930) and Bouckaert and Heymans (1933) for all these and for respiratory gases in the carotid sinus. Later authors (Schmidt, 1932; Bronk and Stella, 1932 and 1935; Gemmill and Reeves, 1933; Samaan and Stella, 1935; Smyth, 1937; Comroe and Schmidt, 1937; and Boyd, 1937) have added many details.

The chemical receptors in mammals are sensitive to oxygen (anoxia) and carbon dioxide tensions of the blood and to certain other chemicals. Bard (1938) impressed by such an unusual position for a receptor for respiratory reflex, states, "It is remarkable that this should be the case, since the corresponding defense against excess CO_2 or acid resides almost entirely in the respiratory centers and does not depend to any great extent on reflexes. There is a possible explanation for this in the embryological development of the carotid sinuses, carotid bodies, and aorta, and though it is purely hypothetical it serves at least to make comprehensible an otherwise inexplicable situation . . . in aquatic vertebrates . . . it is reasonable to suppose that a reflex mechanism to protect against noxious chemical agents could function to best advantage in those parts in which the respiratory exchange takes place with the external environment, and those parts are the gills. . . . Thus we can find a reasonable explanation for the peculiar sensitivity of the carotids and aorta to chemical agents, but what of the respiratory reflexes aroused by changes of pressure in these regions? These also become understandable as another survival of a coordinating mechanism which was of obvious importance in the aquatic vertebrate but which has lost its primitive significance in the air-breathing adult."

The biologist of the lower vertebrates does not have to reason by analogy. Cardiac responses have been obtained from pressure on the branchial vessels of *Squalus*

acanthias (Lutz, 1930a and 1930b, and Lutz and Wyman, 1932a) and on the branchial vessels of *Squalus acanthias* and *Necturus maculosus* (Lutz and Wyman, 1932b) and cardiac inhibition by stimulating the carotid "gland" of the frog (Meyer, 1927). In reptiles and birds as well as in mammals there are innervated structures developed in connection with the third branchial-arch artery and an innervated pressor-receptor zone of the aorta. It is reasonable then to conclude that fish do possess these receptors in the regions of their gills.

As early as 1915 Shelford and Powers found the herring (*Clupea pallasii*) was quite sensitive and responded to water with gradients of carbon dioxide, of oxygenation, of acidity, of fresh-salt water mixtures and of slight temperature differences, and that the humpback salmon (*Oncorhynchus gorbuscha*) was sensitive to gradients of fresh-salt water mixtures. These observations were followed by others by Powers (1921) who showed herring to be quite sensitive to slight gradients of pH. Powers at that time was well aware that pH differences were indices of differences of carbon dioxide tension, as is stated in the body of the paper. And yet these two papers were misunderstood because the same species of fishes were found in wide differences in pH. It has been stated definitely (Powers, Rostorfer, Shipe and Rostorfer, 1938) that "The carbon dioxide tension is the effective factor and not the pH of the water. The pH is incidental to carbon dioxide tension and alkali reserve of each natural water." The ineffectiveness of pH as such had already been discussed by Powers (1930). At this point it is interesting to note that chemical receptors of the carotid bodies are not sensitive to pH—acidity—but to carbon dioxide tension (Samaan and Stella, 1935, and Comroe and Schmidt, 1937). Samaan and Stella state that "The responses to variations of carbon dioxide tension are very prompt."

The fact that the alkali reserve of the blood of a fish is adjusted to the carbon dioxide tension of the water has been shown in various papers by the author and colleagues, and in certain of these it has been shown that the pH of the blood is fairly stable over wide ranges of carbon dioxide tension of the water (Powers, 1922; Powers and Logan, 1925; Powers, Hopkins and Hickman, 1932; Powers, Rostorfer, Shipe and Rostorfer, 1938, and Powers, Rostorfer and Rostorfer, 1939). Finally, it has been shown, despite the fact fishes can adjust the alkali reserve of their blood rapidly to a definite carbon dioxide tension of the water (Powers, 1938) that they become deranged and die if the adjustment is back and forth at too short intervals (Powers, 1937 and 1938; Powers and Rostorfer, 1937, and Powers, Shields and Hickman, 1939).

We have dwelt upon the physiology of fishes since it is applicable to the salmon as well as other fishes. The better the understanding of the physiology, the more likely a true solution to the migratory movements of the salmon will be reached.

There are certain well established facts regarding migratory movements of the salmon. These facts have been established with regard to the (North American) Pacific coast salmon by Gilbert and his associates and others who have followed his methods by checking returns of marked fry and older tagged fish and by the study of scales. The author of this paper will not attempt to discuss the details of the findings of these studies but will leave these to those of this symposium more competent to follow the details. The author will point out more pertinent facts as they relate to his point of view.

The so-called "parent stream theory" has almost become a proverb. Some of the migratory movements of the salmon would be fantastic (Gilbert, 1924) if there were not absolute proof of the facts. All admit that perhaps the majority of the salmon do return to their parent stream. It is also admitted that there is always a certain amount of straying. Davidson (1937) states, "Furthermore, I am not aware of any biologists at the present time thoroughly familiar with the life histories of the Pacific salmon who are of the opinion that any of the species return to their parent streams with unerring accuracy." We all agree (Davidson, 1937) ". . . that the

homing of these salmon is of a sufficient degree to justify conservation measures on the basis of the parent stream principle.'' The differences of opinions come as to the factors involved in the precision with which the salmon do return to the parent stream and as to the factors which bring about straying.

The author will defend his thesis that the guiding factors are the physical and chemical characteristics of the water to which salmon are sensitive and do react and by so doing do reach the spawning grounds, the parent stream. In mammals it has been shown by brilliant, unique, ingenious experimentation, that receptors developed from structures associated with branchial arches are sensitive to carbon dioxide tension, chemicals and low oxygen (anoxia). No doubt it is this response to low oxygen that keeps fishes out of the oxygenless hypolimnion of lakes. Marine fishes including salmon (Shelford and Powers, 1915) do make directive responses to gradients of carbon dioxide tension and of fresh-salt water mixtures. For a more intelligent discussion of the subject, the behavior of the salmon during their migratory movements should be known as well as the physical and chemical characteristics of the water through which they are moving. Unfortunately, little attention has been given to either. The author has obtained information from reliable sources on certain facts concerning the behavior of the red or sockeye (*O. nerka*) and of the king or spring (*O. tschawytscha*) salmon. The king salmon migrates at deeper levels both in the salt water and in the rivers. The reds are often seen ''finning.'' The king does not fin and it keeps in the deeper channels of the river. In the Columbia River the king salmon migrates in the deeper and faster water while the red salmon tends to follow closer to the banks in the less fast and the shallower areas. The fishermen fish for and catch king salmon at greater depths. Some have been caught as deep as 90 fathoms.

In a personal communication to the author Mr. George B. Kelez states as follows:

> The following notes are some observations on the vertical distribution and jumping habits of various species of adult salmon while in the [Puget] Sound and other open waters, and while migrating upstream in large rivers.
>
> These notes do not include observations of salmon while in shallow spawning bed streams, nor do they include fish which have met with obstructions, extremely fast water or rapids. The writer does not feel these observations applicable to this discussion, since under such conditions the fish do not have normal freedom of movement.
>
> Open water observations, made on the fishing grounds, include the Puget Sound, Alaska Peninsula and Bristol Bay areas. Stream observations were made on the Kvichak, Naknek and Egegik Rivers of the Bristol Bay area.
>
> Red Salmon (*O. nerka*)
>
> Open Waters:
>
> Red salmon apparently do not range deeply into the water but stay near the surface. Fishermen find this species can be caught nearer the shore than other species inhabiting the same area. The writer has on several occasions observed small schools swimming not more than three feet under the surface. When found ''gilled'' in the mesh of a purse-seine ''lead,'' these fish tend to go up near the cork line.
>
> Red salmon do not commonly jump in open waters, more frequently they break water with snout and dorsal fin. Among fishermen this exposure is known as ''finning.'' Next to king salmon, reds expose themselves less than other species of salmon.
>
> Upstream:
>
> Here this species tends to keep to the upper three feet of water; they do a small amount of jumping; more frequently they ''fin.''
>
> King Salmon (*O. tschawytscha*)
>
> Open Waters:
>
> King salmon are caught by commercial trollers, fishing at a depth of 30 to 40 fathoms or even deeper. To the writer's knowledge, this species has not been observed swimming near the surface. It is rare to see this species jump.
>
> Upstream:
>
> Kings were observed swimming deeper than reds or chums in the same area. They were neither observed jumping nor ''finning.''[1]

[1] The information concerning the behavior of the salmon was obtained through the kindness of Dr. F. A. Davidson, Director, Seattle, Washington, Bureau of Fisheries; Mr. George B. Kelez, Acting Director, Seattle, Washington, Bureau of Fisheries, and Mr. Richard T. Smith of the Washington State Fisheries Department. Mr. Kelez was for some years engaged on a red salmon research problem on the Chigniti river and lakes, Alaska. Mr. Smith has had first hand information in fishing.

Of the two fishes, the red salmon, when there is a choice, will choose the fork of a river which drains a lake. The other, the king salmon, does not choose between the two forks but will move up either one or the other.

We will now consider accurate observations made on these two species of salmon and see if the characteristic behaviors can in any way be correlated with their migratory movements and distribution.

The most interesting as well as the most instructive tagging experiments (Fig. 1) are those reported by Gilbert (1924) and Gilbert and Rich (1927a). Red salmon were tagged in Ikatan Bay (entrance to Isanotski Strait), Morzhovoi Bay (just east of Ikatan Bay) and Unga Island of the Shumagin Islands group (some 125 miles east of Ikatan Bay). All three tagging localities are on the south side of the Alaskan Peninsula. Not a single red salmon tagged in either of the bays was captured on the south side of the peninsula east of Morzhovoi Bay. Those that were not captured in one or the other of the two bays were captured north of the peninsula and to the east along the margin of and in rivers emptying into Bristol Bay. A few were captured at Port Moller, about one-third down toward Bristol Bay on the north side of the peninsula. Red salmon tagged at Port Moller were not captured outside its waters. Results were different with the Unga Island experiments. The majority of the recaptures were along the route to Isanotski Strait and at approximately the same localities as previously in Bristol Bay. A small per cent of returns were east along the south of the peninsula as far as Cook Inlet. According to Gilbert and Rich (1927b), "two of the best-known red salmon streams in Alaska are the Karluk River, on Kodiak Island and the Chignik River" on the south shore of the peninsula about half way between Kodiak Island and the Shumagin Islands. ". . . their runs are nowhere subject to any considerable commercial capture except in the vicinity of their respective mouths." There is no doubt that some of the red salmon in the waters in the vicinity of these two rivers, but not close in, move toward the east. Red salmon tagged at Unga Island were captured as far east as Cook Inlet and must have passed these two rivers, but again not close in. The author has found no observations in any paper that he has read (see bibliography), that indicates the salmon east of the Shumagin Islands ever move west.

When it is learned that there is a current, or at least a drift, from Bristol Bay toward the west, and a part of this water passes from Bering Sea through Isanotski Strait into the Pacific Ocean these observations just recounted take on a new light.[2] Going into further detail, the Cape Pankof Peninsula, and to a less extent, Sanak Island constitute a barrier to the west and Thin Point and Deer Island constitute a more efficient barrier on the east to the Ikatan and Morzhovoi Bays area (Fig. 1). Thus, waters from Bering Sea (Bristol Bay region) would spread giving a very slight gradient of these waters—a fresh-salt water gradient. This gradient would be so delicate, and quite often interrupted by waters coming in from outside through the not complete barriers just mentioned, that the red salmon would be retained in this area some time (some fish as long as three weeks or so according to Gilbert, 1924, and Gilbert and Rich, 1927a). At no time would these fish leave this area to the south, west or east, since there would always be a more or less steep salt-fresh water gradient between the waters of this area and the less diluted sea water constituting the westward oceanic drift of the Pacific. After

[2] Captain G. S. Bryan, United States Navy, personal communication states, "While there have never been extensive studies made of the currents in the Bering Sea, according to the U. S. Coast Pilot, Alaska, Part II, 1931, the current in Bering Strait sets northward with a normal velocity of about two knots. The currents in Bristol Bay are usually considered as partly tidal, although a strong northeast storm will cause a strong current to sweep out of the bay. Aside from tidal influences, there is a permanent eddy that enters past Cape Newenham, flows eastward and discharges along the north shore of Unimak Island flowing westward."

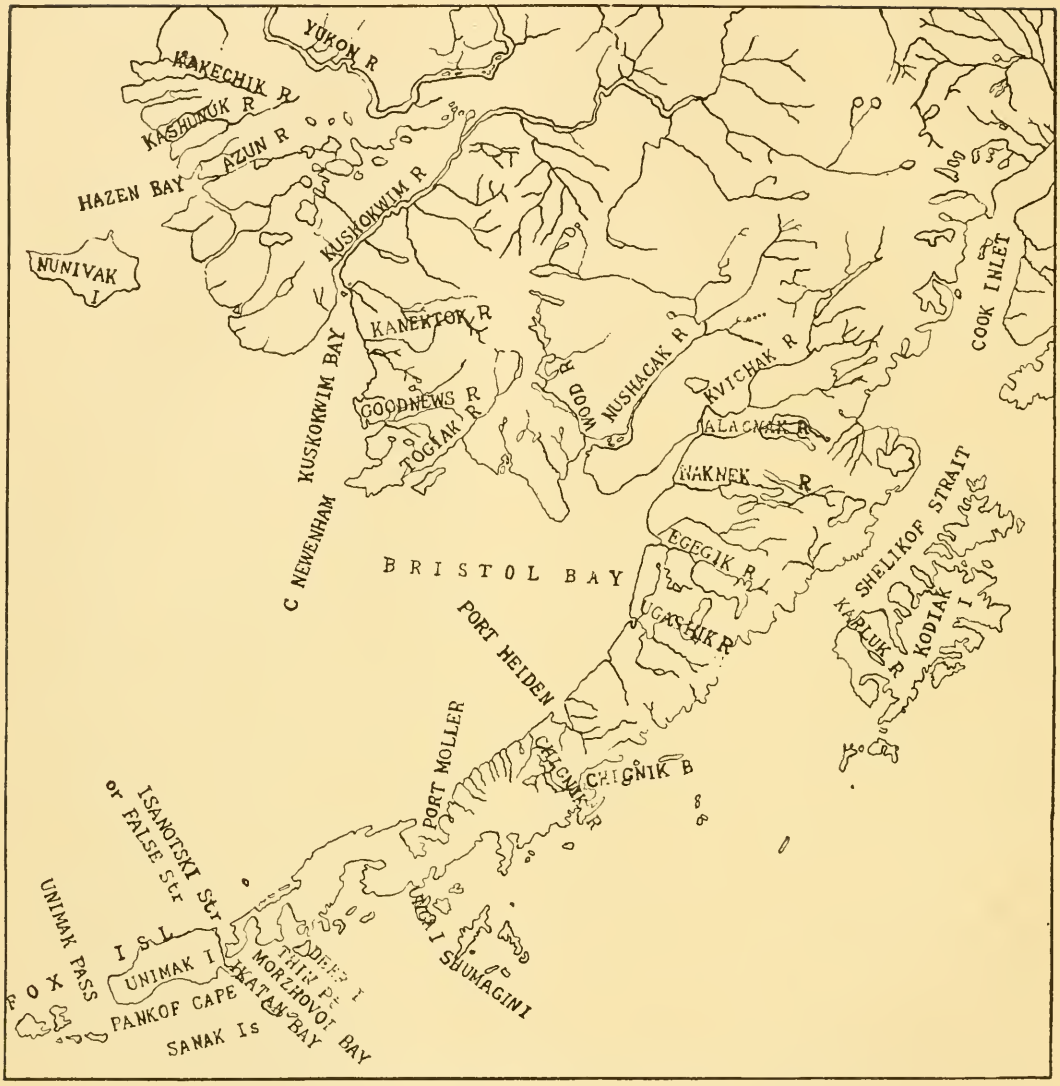

FIG. 1. THE ALASKA PENINSULA AND BRISTOL BAY REGIONS.

a longer or shorter time the fish would be caught in a stronger fresh-salt water gradient and move through Isanotski Strait into Bering Sea. Once in Bering Sea the fresh-salt water gradient is toward the Bristol Bay streams from which there is a westward drift to Unimak Pass and westward but some of the water passing through Isanotski Strait to the Pacific. When the red salmon reach Bering Sea, they, according to observations (Gilbert, 1924, and Gilbert and Rich, 1927a) lose no time in reaching a spawning ground area. All waters emerging from Isanotski Strait have been thoroughly mixed. All will agree with and none can object to this statement. In short, there is an irregular fan-shaped fresh-salt water gradient from Isanotski Strait to the Bristol Bay area. The red salmon not destined to any particular stream are following a gradient which at times is quite irregular. A fish may be following a gradient dominated at the time by one stream and for one reason or another be switched to a gradient dominated by an entirely different stream. Now, the Shumagin Islands can

not be a complete barrier to the west drift on the Pacific Ocean side of the Peninsula. However, it is a barrier sufficient to divert a large part of this water to the south and to allow a drift from the Ikatan and Morzhovoi Bays area. Thus, east of the Shumagin Islands the fresh-salt water gradient would be from the east, of necessity, since the current or drift is from this region. The Shumagin Islands region is the parting of the ways of the west and east fresh-salt water gradients and is also the parting of the ways of the red salmon's migratory movements. No doubt red salmon pass through Unimak Pass and even westward on their way to Bristol Bay. Tagging observations and the westward drift of the ocean current would lead one to conclude that the red salmon which pass through Unimak Pass and west do not come from the east but from the west feeding grounds, and would lose no time in reaching spawning ground areas. That is, at no place would they be delayed as in Morzhovoi and Ikatan Bays and form a good fishing ground.

What is the gradient to which the red salmon is reacting? Let us now consider the observations made by Gilbert and Rich (1927b) on Karluk River, Kodiak Island, one of the two best red salmon streams in Alaska. The other is the Chignik River which is west and on the Pacific Ocean side of the Peninsula. Even though the red salmon may respond to a fresh-salt sea water gradient out in the open ocean, this cannot be true after it has entered a river proper. Still the red salmon is quite selective of the streams flowing into Karluk Lake. The best spawning streams are: Salmon Creek "a tributary of some size comes brawling in . . . is a favorite spawning ground for red salmon. Far more spawn in this stream than in Thumb Lake or all of the other tributaries"; Fall Creek ". . . the majority went into Fall Creek . . . the stream grows boisterous"; "Canyon Creek of real value . . . it enters hilly country, has a swift current and rocky floor . . ."; and "two short creeks, Grassy Point Creek and Halfway Creek . . . are brawling streams, with coarse boulder beds and only occasional very limited patches of gravel . . . but in spite of their small size and unfavorable character they carry more red salmon in proportion to their size than do the more suitable spawning streams of the Thumb and head of lake." What are the common characteristics of the better spawning streams? The first and perhaps most important characteristic is that all are boisterous streams. This assures a carbon dioxide tension of the water approximating the carbon dioxide partial pressure of the air. From these observations one is led to suspect that the red salmon, at least after having entered a stream, are responding to the carbon dioxide tension of the water. Further evidence will be presented that will show that this supposition is most probably correct.

Other observations on the inshore tagging of red salmon dominated by gradients of fresh water from streams near at hand (Rich and Suomela, 1927) show that red salmon as well as other species scatter, *i.e.*, move to different spawning grounds from one and the same tagging station. This same tendency is shown to be true (Davidson and Christley, 1938) in the case of the pink salmon (*O. gorbuscha*). The most interesting fact is that none of the salmon tagged in close proximity (marked gradients to streams) ever strayed to streams beyond this proximity—outside and beyond their gradients.

When the tagging experiments carried on in Canadian waters (Pritchard, 1930; Clemens, 1930; Williamson, 1927; Williamson and Clemens, 1929 and 1932; Clemens, 1932; Pritchard, 1932, 1934a and 1934b) are examined one is struck by the predominant movements toward the south of all species of salmon tagged. When the tagged salmon moved north in the waters east of Vancouver Island, or even on the west side for that matter, and in the water at and near to Queen Charlotte Islands, it would be interesting to know just what were the effects of the tides and other factors in changing gradients of fresh-salt water mixtures. We find the fol-

lowing statement by Davidson and Christley (1938) that "These salmon no doubt migrated across Clarence Strait to the west shores of Gravina and Annette Islands and then turned back to the localities on the east shore of Prince of Wales Island in area 2. Whether or not the salmon make this journey may depend to some extent upon the prevailing winds. If a southeast wind is blowing the opposite course is more apt to be taken. No definite conclusions may be drawn because of the lack of sufficient information, at the present time, concerning the influence of wind direction on migration." There is no doubt that wind can divert the flow of the less mixed fresh-salt waters at the surface. This being the case the direction of the gradient to which salmon responds would be changed; thus, the change in the path of the movement of the salmon.

From tagging experiments and otherwise the king salmon is known to make the longest and most extensive migratory movements when at sea. It also moves deepest below the surface. The fresh-salt water mixture at depths at which the king salmon migrates would be more stable and less modified by the tide.

A more crucial test of the theory that the salmon find their spawning grounds by reacting to environmental factors is to compare the behaviors of the red and king salmon as they ascend the rivers to their spawning grounds. In fresh water the king salmon still moves at greater depth than the red salmon. The red salmon moves at and near the surface of the water. When a choice must be made between two forks of a river the red salmon is said to choose the fork having a lake above. The king salmon is said to be indifferent in the choice. Powers (1928) and Powers and Hickman (1928) found that in the Fraser and Columbia River systems the fork of the river with a lake above always had a carbon dioxide tension nearest the carbon dioxide partial pressure of the atmosphere. This is not only true according to observation but it is most reasonable. Surfaces of lakes are well aerated. Most spring and seep water as a general rule contain carbon dioxide at a higher tension than the carbon dioxide partial pressure of the atmosphere. This, with the Karluk Lake observation (Gilbert and Rich, 1927b) where the red salmon spawned in the streams with best aerated water, leaves one to conclude that the red salmon responds positively to a carbon dioxide tension nearest the carbon dioxide partial pressure of the atmosphere. This is also reasonable since the red salmon moves nearest the surface and at times near shore in rivers where the carbon dioxide tension would be most nearly in equilibrium with the carbon dioxide partial pressure of the atmosphere. Even though chemical receptors located in the regions of the gills were not sensitive to changes in carbon dioxide tension the alkali reserve of the blood would have to be modified in order to be adjusted to the new carbon dioxide tension. The adjustment would be least if the red salmon chose the water having a carbon dioxide tension most nearly the same carbon dioxide tension of the water in which it had been moving. There are abundant data that show that a fish's blood is continuously adjusting its alkali reserve to the carbon dioxide tension of the water. The king salmon may or may not respond to a carbon dioxide tension gradient. The alkali reserve in its blood can be adjusted up or down. The advantage would be in the water requiring the least adjustment. This would depend upon the relative volumes of the two waters making up the mixture. This would in turn depend upon the volume of the two streams and the position of the king salmon in the mixed waters below the forks. Thus, the king salmon could be said to be indifferent to the change in the carbon dioxide tension, though its choice between the two forks would depend upon its position in the stream below the two forks.

A very important observation made by Ward (1921) was that red salmon in the Copper River system enter streams that do not have any lake above. The salmon always chose a stream having a lower temperature. The Copper River is supplied

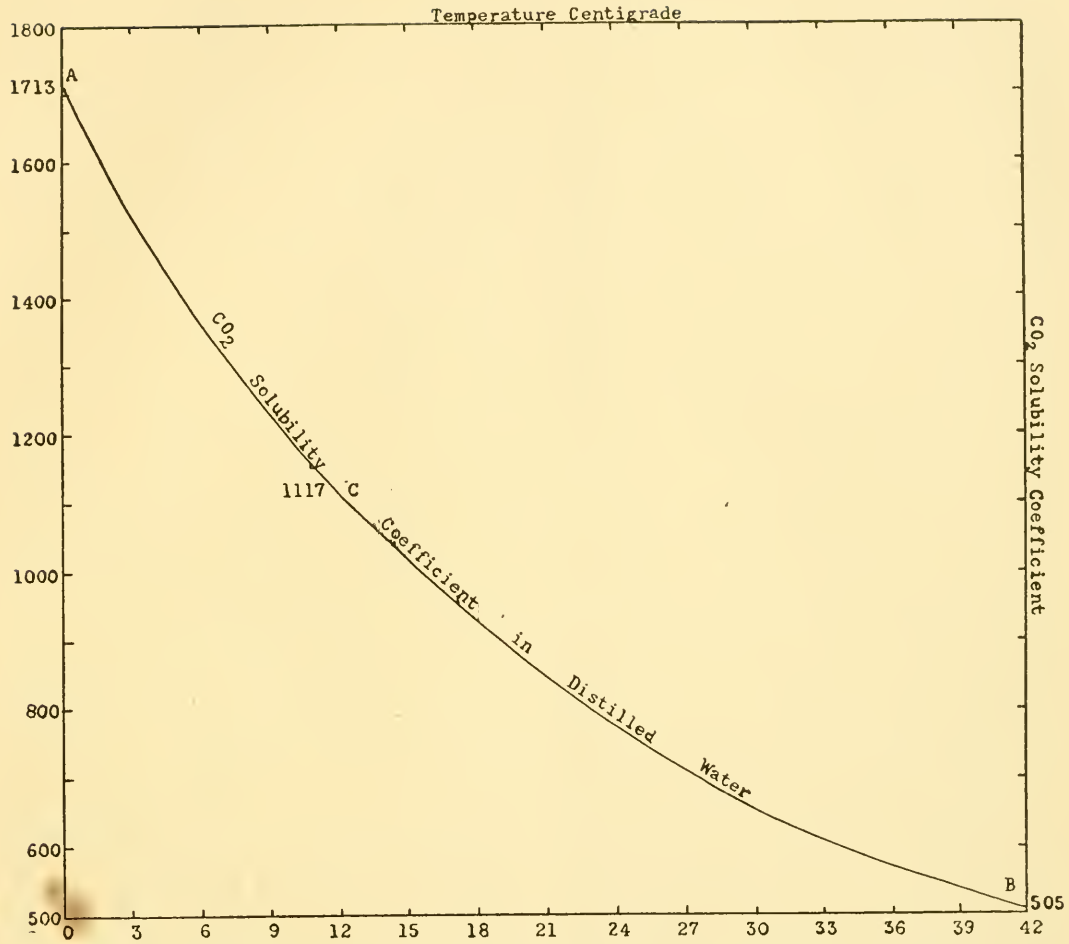

FIG. 2. CURVE AB REPRESENTS THE RELATION BETWEEN THE CARBON DIOXIDE SOLUBILITY COEFFICIENT IN DISTILLED WATER AND TEMPERATURE. THE POINT C IS THE SOLUBILITY OF CARBON DIOXIDE AT 12° C.

with glacier water. The seep and spring water could not be of deep origin since the ground never thaws to any great depth. It would be logical to suppose that the carbon dioxide tension of the water of Copper River would approximate the carbon dioxide partial pressure of the atmosphere. If this be true, the colder the water the lower its carbon dioxide tension (the heating of water without loss of carbon dioxide increases its carbon dioxide tension). Thus, the salmon could be reacting to carbon dioxide tension at the same time that it was reacting to temperature. Regardless of what the fish was responding to, these observations (Ward, 1921) are proof that the red salmon can and does react to factors of its environment.

A more crucial test is the results of artificial planting of the Pacific coast salmon. Davidson and Hutchinson (1938) have treated this subject in an excellent manner. Of some 15 and more repeated attempts to plant the Pacific coast salmon *Oncorhynchus,* only five have been successful in developing natural populations with characteristics similar to those in their native distribution. These authors have summarized the situation of the development of natural populations.

"The environmental components, as considered in this study of the foreign streams

and lakes and coastal waters in which these salmon have developed natural runs, have in every case been similar to the components of the waters frequented by the salmon in their native range. On the other hand, the environmental components of the foreign waters in which these salmon have failed to develop natural runs have differed from those of the waters native to the salmon." (Davidson and Hutchinson, 1938.)

Aside from the fact that environmental conditions must be favorable three other facts are outstanding. First, certain streams in South Island, New Zealand, have been frequently stocked with *O. tschawytscha* (chinook, quinnat or king) but have never developed natural runs. This is also true of North Island in which no natural runs have developed. Second, "Not a single individual of the quinnat species has ever been planted in a Canterbury stream, yet the Canterbury rivers now provide the best quinnat fishing in the Dominion, the species having migrated to their mouths from the Waitaki where the original fry were planted." Third, the red salmon "eggs were imported in 1902 . . ." " 'a number (red salmon) exist in Lake Chan, having acquired a land locked habit. These fish run up creeks at the head of the lake and spawn there every season (year) in March and April'."

In South Island, New Zealand, we have (1) streams being stocked without producing runs, (2) an *adopted parent* stream and (3) red salmon becoming land locked after being planted and not developing natural runs.

The first proves that if the environmental conditions are not right the salmon will not return (stray) to the stream of its origin. The second proves that salmon, provided the proper gradient is present will move to a stream regardless of the fact that neither it nor any ancestor has ever visited or originated in the stream. As to the land locking of the red salmon, Professor Ward (1932) has given the best and perhaps the only explanation.

Environmental factors cause the salmon to migrate to the sea. Response to environmental factors in the case of the land locked salmon holds them in a lake. It is a striking coincidence that there is no regular run of salmon into a land locked salmon lake and vice versa. Ward, from the first, has attacked the problem of salmon migration from the point of view that the salmon is responding to environmental factors (Ward 1921, 1927, 1929, 1930 and 1932). His observations are in agreement with those of the author. The carbon dioxide tension of the waters, which are agitated in their rapid descent from the glacial snowfields, are necessarily approximately in equilibrium with the carbon dioxide partial pressure of the atmosphere. The temperature of these waters is continuously being raised by the heat of the summer sun (Dall, 1882). The carbon dioxide solubility coefficient of water is lowered with rise in temperature. Hence, the liberation of carbon dioxide from the water would always lag behind the rise of temperature. Therefore, at the same time that the red salmon is moving toward a lower temperature, it is also responding to a lower carbon dioxide tension of the water. Figure 2 demonstrates the relation of temperature to the carbon dioxide solubility coefficient in distilled water. If the temperature of the water were suddenly raised to 12° C. without loss of carbon dioxide, its carbon dioxide tension would suddenly be raised approximately 53 per cent.

Two questions now remain, first, to what extent do salmon return to the stream (spawning grounds) in which they actually originated? And, second, why do the salmon go out to sea? In connection with the first it is maintained that each spawning ground gives rise to a definite race. This is difficult to get around. However, there has been much doubt as to the validity of these claims as to the distinctness of races (Huntsman, 1937a and 1937b). Let us examine once more the tagging experiments carried on east of the Alaska Peninsula at points from Ikatan Bay to Unga Island (Gilbert and Rich, 1927a), since the returns from these experiments are unique but analyzable. The salmon tagged are,

"in the midst of their migration in the sea, far from the spawning streams toward which they are directing their course."

Salmon ". . . associated in the same trap on Unga Island . . . scattered to more than 20 different streams, ranging from Cook Inlet on the south to Goodnews Bay, the Kuskokwim, and the mouth of the Yukon in the far north." It is true that "The physical and chemical conditions of their immediate environment assuredly were identical for all the salmon tagged and released at a given time from a single trap." The guiding influence is a response to factors associated with a fresh-salt water mixture. Dall (1882) states, "the Kuskokwim and Bristol Bay rivers discharge more to the southward, the result being a southwest or southeast set of the waters near them, according to the prevailing wind and tide." He mentions "this general southerly set of the southeast part of Bering Sea," as having been "observed by various navigators." These observations show that there are gradients from the tagging station to the spawning grounds to which salmon were directed.

If salmon move to sea, as it has been abundantly proved that they do, why do they reverse their response and return to the spawning grounds? Much excellent work has been done on both sides of the Atlantic. Again the migratory movements of the Pacific salmon are most easily analyzable. The tagging experiments with the Pacific salmon seem to prove that the feeding salmon drift with the ocean current since the returns from outside the immediate influence of a stream is southward, that is, against the ocean current. The extent of this drift at the present time must be purely speculative. However, there has been no evidence that a salmon which does return has drifted beyond the influence of the inshore waters that mingle with the offshore waters to form the ocean drift waters. This offshore water has two characteristics. First, the sea water is mixed with fresh water. Second, this offshore water must have a lower carbon dioxide tension during spring and summer than the ocean water due to the photosynthesis of the more intense population of phytoplankton and to the sea weeds of the continental shelf. These two factors alone might keep the salmon within their influence. Why do salmon approaching sexual maturity return along definite paths to the spawning grounds? The ova and sperm heads contain a protein (protamine) containing large percentages of arginine. It requires a vast protein metabolism to obtain the necessary arginine. Protein metabolism and especially fasting—both necessary for the liberation of arginine from the muscular tissue of the salmon—tends to produce acidosis of the blood, *i.e.*, lower the alkali reserve of the blood. This is common knowledge. A salmon with a low alkali reserve blood would find low carbon dioxide tension water more advantageous. We have presented evidence if not proof (see bibliography) that fish do have receptors in their gills sensitive to carbon dioxide tension. Due to photosynthesis there must be a gradient of carbon dioxide tension from inshore to offshore waters. The salmon in its return is responding to the carbon dioxide tension gradient or a fresh-salt water gradient. There is again evidence that the salmon is reacting to a carbon dioxide gradient at least inshore. Ward (1927) states, ". . . the coastal streams which are utilized by the Pacific salmon come out of the mountains near the shore. They are characterised by rapid flow of water and considerable drop within a short distance. In the main, they are fed by glaciers or snow fields of the high mountains so that the water temperature is relatively low and the water flow in summer high." Streams of this type have low carbon dioxide tension water. It has been shown by actual observation (Powers, 1928, and Powers and Hickman, 1928) that the waters of the Columbia and Fraser River systems have relatively low carbon dioxide tensions.

In order that there be a directive response there must of necessity be a gradient of the factor or factors to which the salmon are responding. It is not the contention of

the author that salmon do not respond to factors other than gradients of carbon dioxide tension and fresh-salt water. There are many other factors, food, etc. These many responses are the factors that keep the salmon distributed throughout their habitats. If gradients of factors to which salmon respond are not sufficiently steep to direct the movements of the salmon they might move about seemingly aimlessly and thus be carried by the ocean drift (Huntsman, 1938b). To illustrate, if fish responded to current only they would all be at the heads of streams and not distributed throughout the streams.

The movements of fishes, of necessity more than of any other vertebrate, are dominated by responses to the environment. The first development of a cortex from the pallium appears in the amphibia. The cerebra of the fish are mainly corpora striata and olfactory bulbs. The cortex reaches its highest development in mammals (man) and the highest level of the corpora striata is reached in birds. We will not discuss the relative exactness of the migratory movements of these two classes of vertebrates.

Greene (1915, 1918 and 1919) has shown that in the king salmon the muscle protein is reduced about 30 per cent and the fat from 18 per cent to as low as 1.6 per cent during its spawning migratory movements from the brackish water to the spawning grounds. The weights of the ovaries are (Greene, 1921) in brackish water 501 to 749 gm, in spawning beds 775 to 2,243 gm and when ripe 2,596 gm. The average depression of the freezing point of the blood (Greene, 1905) is $-0.762°$ C for sea salmon, $-0.737°$ C for brackish water and $-0.628°$ C for spawning ground salmon.

Questions that can legitimately be asked are: Does the electrolyte content of the blood change with the salt content of the environment and is the salmon held back until this change has taken place in the blood before ascending the river? Or is the electrolyte content of the blood lowered in coordination with the special metabolism in the ripening of the germ cells and is the salmon held back until this change has taken place in the blood before ascending the river? Observations indicate that the second series of events is the more probable. The more nearly ripe the germ cells the shorter the time the salmon lingers in the brackish water before ascending the river. When the germ cells are ripe or nearly ripe the salmon loses no time in passing from the brackish water to fresh water or ascending the river to the spawning ground.

Huntsman (1936, 1938a, 1938b, and 1938c) presents evidence that the Atlantic salmon never gets beyond the influence of the fresh water. That is, a salmon never passes into pure oceanic water and still finds its way back to fresh water. A delay in the salmon's passage from fresh water to salt water and the second delay in its passage from brackish water to fresh water both favor the view here presented. That is, the state of the metabolism of the salmon determines the extent of its movements into waters of greater salt contents. The fact that salmon do not ordinarily leave the salt water and ascend the rivers except when the germ cells are ripening (that is, there are one year, two year, three year, etc., periods in the sea) lends weight to the view that the state of metabolism determines the vigor or intensity of the response of the salmon to the environment. The mature respond more vigorously than the immature to fresh-salt water and carbon dioxide tension (one or the other or both) gradients.

To summarize, in order that there be a directive response there must of necessity be a gradient of the stimulating factor or factors. Evidence from the most exact observations indicates that the salmon which do return never move beyond the influence of fresh water. There are two possible gradients, a fresh-salt water gradient and a carbon dioxide tension gradient. Time will tell which of the two gradients dominates the spawning migratory movements of the salmon from the sea to the fresh water. At the present time the evidence seems to favor the carbon dioxide tension gradient. However, the fresh-salt

water gradient is not without effect, as is shown by the delay of the fresh-salt water passage of the salmon to and from the salt water. Other evidence favoring the carbon dioxide tension gradient is that the response is seasonal with both mature and immature salmon as is the carbon dioxide tension gradient. The physiological evidences favoring the carbon dioxide tension gradients are (1) the presence of receptors in the morphological regions of the gills among vertebrates sensitive to carbon dioxide tension as such and (2) the special type of metabolism necessary for the ripening of the germ cells. Finally, the red salmon seems to be responding to a carbon dioxide tension gradient in its movements when in the fresh water and when selecting a spawning ground.

Summary

1. Chemical receptors sensitive to carbon dioxide tension are found in the branchial arches or in structures derived from branchial arches.

2. It has been shown in the laboratory that fishes including salmon respond to gradients of physical and chemical characteristics of the water.

3. Tagging experiments in Alaskan waters have shown that the red salmon migrate to the spawning grounds along paths of fresh-salt water gradients.

4. The red salmon as a rule choose the fork of the river that drains a lake.

5. Rivers draining lakes, as has been shown by actual observation, have carbon dioxide tensions more nearly in equilibrium with the carbon dioxide partial pressure of the air than do spring-fed rivers.

6. Streams having the most vigorously aerated (low carbon dioxide tension) water are chosen as spawning grounds by the red salmon as is shown by observations made on the Karluk River system.

7. These views are further supported by the fact that the greatest number of all species of salmon are moving against the ocean current (drift) during their spawning migration.

8. It is suggested that the movements into the sea are largely drifts and at the same time the salmon are held within the bounds of a fresh-salt water gradient.

References Cited

Bard, P. 1938. Macleod's Physiology in Modern Medicine. St. Louis.

Barnes, T. C. 1937. Textbook of General Physiology. Philadelphia.

Bouckaert, J. J., and Heymans, C. 1933. Carotid Sinus Reflexes. Influence of Central Blood Pressure and Blood Supply on Respiratory and Vaso-motor Centers. *J. Physiol.*, 79: 49–66.

Boyd, J. D. 1937. The Development of the Human Carotid Body. *Carnegie Inst. Washington*, 26: 1–31.

Bronk, D. W., and Stella, G. 1932. Afferent Impulses from Single End Organs in the Carotid Sinus. *Proc. Soc. Exper. Biol. and Med.*, 29: 443.

———. 1935. The Response to Steady Pressures of Single End Organs in the Isolated Carotid Sinus. *Amer. J. Physiol.*, 110: 708–714.

Clemens, W. A. 1930. Pacific Salmon Migration. The Tagging of the Coho Salmon on the East Coast of Vancouver Island in 1927 and 1928. *Biol. Board of Can., Bull.* 15: 1–19.

———. 1932. Pacific Salmon Migration. The Tagging of the Spring Salmon on the East Coast of Vancouver Island in 1927 and 1928 with Notes on Incidental Tagging of Other Fish. *Biol. Board of Can., Bull.* 27: 1–10.

Comroe, T. H., and Schmidt, C. F. 1937. Reflexes from the Carotid Body (*Glomus Caroticum*) to the Respiratory Center of the Dog. *Amer. J. Physiol.*, 119: 290–291.

Cyon, E., and Ludwig, C. 1866. Die Reflexe eines der sensibilen Nerven des Herzens Auf die motorischen der Blutgefässe. *Ber. Verh. k. Sächs. Gesell. Wiss. Leipzig, Math.-Phys. Cl.*, 18: 307–328.

Dall, W. H. 1882. Report on the Currents and Temperatures of Bering Sea and the Adjacent Waters. *U. S. Coast and Geodetic Survey, Report*, 1880: 297–340.

Davidson, F. A. 1937. "Migration" and "Homing" of Pacific Salmon. *Science*, 86: 1–4.

Davidson, F. A., and Christley, L. S. 1938. The Migrations of Pink Salmon (*Oncorhynchus gorbuscha*) in the Clarence and Summer Straits Regions of Southeastern Alaska. *Bull. U. S. Bur. Fish.*, 48: 643–666.

Davidson, F. A., and Hutchinson, S. J. 1938. The Geographic Distribution and Environmental Limitations of the Pacific Salmon (Genus *Oncorhynchus*). *Bull. U. S. Bur. Fish.*, 48: 667–692.

Gemmill, C. L., and Reeves, D. L. 1933. The Effect of Anoxemia in Normal Dogs before and after Denervation of the Carotid Sinuses. *Amer. J. Physiol.*, 105: 487–495.

GILBERT, C. H. 1924. Experiments in Tagging Adult Red Salmon, Alaska Peninsula Fisheries Reservation, Summer of 1922. *Bull. U. S. Bur. Fish.*, 39: 39–50.

GILBERT, C. H., AND RICH, W. H. 1927a. Second Experiment in Tagging Salmon in the Alaska Peninsula Fisheries Reservation, Summer of 1923. *Bull. U. S. Bur. Fish.*, 42: 27–75.

————. 1927b. Investigations Concerning the Red Salmon Runs to the Karluk River, Alaska. *Bull. U. S. Bur. Fish.*, 43: Pt. II: 1–69.

GREENE, C. W. 1905. Physiological Studies of the Chinook Salmon. II. A Study of the Blood and Serous Liquids by the Freezing Point Method. *Bull. U. S. Bur. Fish.*, 24: 445–456.

————. 1915. On Some Quantitative Physiological Changes in the Pacific Salmon During the Run to the Spawning Grounds. *Trans. Amer. Fish. Soc.*, 45: 5–12.

————. 1918. The Composition of the Ovaries of the Salmon During Migration. *J. Biol. Chem.*, 33: XIII–XIV.

————. 1919. Biochemical Changes in the Muscle Tissue of King Salmon During the Fast of Spawning Migration. *J. Biol. Chem.*, 39: 435–456.

————. 1921. Chemical Development of the Ovaries of the King Salmon During the Spawning Migration. *J. Biol. Chem.*, 48: 59–71.

HERING, H. E. 1924. Der Sinus caroticus an der Ursprungsstelle der Carotis interna als Ausgangsort eines hemmenden Herzreflexes und eines depressorischen Gefässreflexes. *Münch. Med. Wochenschr.*, 71: 701–704.

HEYMANS, J. F., AND C. 1927. Sur les modifications directes et sur la regulation reflexe de l'activité du centre respiratoire de la tête isolée du chien. *Arch. Internat. de Pharmacodyn. et de Therap.*, 33: 273.

HEYMANS, C., AND BOUCKAERT, J. J. 1930. Sinus Caroticus and Respiratory Reflexes. *J. Physiol.*, 69: 254–266.

HUNTSMAN, A. G. 1936. Return of Salmon from the Sea. *Biol. Board Can., Bull.* 51: 1–20.

————. 1937a. "Races" and "Homing" of Salmon. *Science*, 85: 582–583.

————. 1937b. "Migration" and "Homing" of Salmon. *Science*, 85: 313–314.

————. 1938a. Sea Movements of Canadian Atlantic Salmon Kelts. *J. Fish. Res. Board Can.*, 4: 96–135.

————. 1938b. "Spawning Urge," "Homing Instinct" and "Waiting" in Salmon Return. *Nature*, 141: 421–423.

————. 1938c. Sea Behaviour in Salmon. The Case Against an Hereditary Homing Instinct. *Salmon and Trout Magazine*, 90: 1–5.

LUTZ, B. R. 1930a. Reflex Cardiac and Respiratory Inhibition in the Elasmobranch, *Scyllium canicula*. *Biol. Bull.*, 59: 170–178.

————. 1930b. The Innervation of the Heart of the Elasmobranch, *Scyllium canicula*. *Biol. Bull.*, 59: 211–216.

LUTZ, B. R., AND WYMAN, L. C. 1932a. The Evolution of a Carotid Sinus Reflex and the Origin of Vagal Tone. *Science*, 75: 590–591.

————. 1932b. Reflex Cardiac Inhibitions of Branchio-vascular Origin in the Elasmobranch, *Squalus acanthias*. *Biol. Bull.*, 10–16.

MEYER, F. 1927. Versuche über Blutdruckzügler beim Frosch. *Pflüger's Arch. f. d. ges. Physiol.*, 215.

POWERS, E. B. 1921. Experiments and Observations on the Behavior of Marine Fishes Toward the Hydrogen-ion Concentration of the Seawater in Relation to Their Migratory Movements and Habitat. *Publ. Puget Sound Biol. Sta.*, 3: 1–22.

————. 1922. The Physiology of the Respiration of Fishes in Relation to the Hydrogen-ion Concentration of the Medium. *J. Gen. Physiol.*, 4: 305–317.

————. 1928. The Carbon Dioxide Tension, Oxygen Content, the pH and the Alkali Reserve of Natural Waters Mostly of the Western Portion of the United States. *Publ. Puget Sound Biol. Sta.*, 5: 381–391.

————. 1930. The Relation between pH and Aquatic Animals. *Amer. Nat.*, 64: 342–366.

————. 1937. Notes on Mortality of Fish at Kephart Prong Fish Rearing Pools. *J. Tenn. Acad. Sci.*, 12: 309–315.

————. 1938. The Factors Involved in the Sudden Mortality of Fishes. *Trans. Amer. Fish. Soc.*, 67: 271–281.

POWERS, E. B., AND HICKMAN, T. A. 1928. The Carbon Dioxide Tensions of the Fraser River and Its Lower Tributaries and of Certain Tributaries of the Columbia River. *Publ. Puget Sound Biol. Sta.*, 5: 373–380.

POWERS, E. B., HOPKINS, F. G., AND HICKMAN, T. A. 1932. The Relation of Respiration of Fishes to Environment. IV. Relation of Carbon Dioxide and Oxygen Contents of the Blood to the Carbon Dioxide and Oxygen Tensions of the Environmental Water. *Ecol. Monog.*, 2: 396–414.

POWERS, E. B., AND LOGAN, G. A. 1925. The Alkaline Reserve of the Blood Plasma of the Viviparous Perch (*Cymatogaster aggregatus* Gib.) in Relation to the Carbon Dioxide Tension, the Oxygen Tension and the Alkalinity of the Sea Water. *Pub. Puget Sound Biol. Sta.*, 3: 337–360.

POWERS, E. B., ROSTORFER, H. H., AND ROSTORFER, T. H. 1939. The pH, Carbon Dioxide Tension, and the Hemoglobin Percentages of Venous Blood of Various Fresh Water Fishes. *Ohio J. Sci.*, 539: 1–9.

POWERS, E. B., ROSTORFER, H. H., SHIPE, L. M., AND ROSTORFER, T. H. 1938. The Relation of Respiration of Fishes to Environment. XII. Carbon Dioxide as a Factor in Various Physiological Respiratory Responses in Certain Fresh Water Fishes. *J. Tenn. Acad. Sci.*, 13: 220–245.

POWERS, E. B., AND ROSTORFER, T. H. 1937. The Mortality of Fish at the Hamblem State Hatchery. *J. Tenn. Acad. Sci.*, 12: 377–380.

POWERS, E. B., SHIELDS, A. R., AND HICKMAN, M. E. 1939. The Mortality of Fishes in Norris Lake. *J. Tenn. Acad. Sci.*, 14: 239–260.

PRITCHARD, A. L. 1930. Pacific Salmon Migration: The Tagging of the Pink Salmon and the Chum Salmon in British Columbia in 1928. *Biol. Board Can., Bull.* 14: 1–17.

————. 1932. Pacific Salmon Migration: The Tagging of the Pink Salmon and the Chum Salmon in British Columbia in 1929 and 1930. *Biol. Board Can., Bull.* 31: 1–16.

————. 1934a. Pacific Salmon Migration: The Tagging of the Coho Salmon in British Columbia in 1929 and 1930. *Biol. Board Can., Bull.* 40: 1–24.

————. 1934b. Pacific Salmon Migration: The Tagging of the Spring Salmon in British Columbia in 1929 and 1930. *Biol. Board Can., Bull.* 41: 1–31.

RICH, W. H. 1926. Salmon Tagging Experiments in Alaska, 1924 and 1925. *Bull. U. S. Bur. Fish.*, 42: 109–146.

————. 1935. Salmon Tagging Experiments in Alaska, 1930. *Bull. U. S. Bur. Fish.*, 47: 399–406.

RICH, W. H., AND BALL, E. M. 1935a. Statistical Review of the Alaska Salmon Fisheries. Part III. Prince William Sound, Copper River and Bering River. *Bull. U. S. Bur. Fish.*, 47: 187–247.

————. 1935b. Statistical Review of the Alaska Salmon Fisheries. Part IV. Southeastern Alaska. *Bull. U. S. Bur. Fish.*, 47: 437–662.

RICH, W. H., AND MORTON, F. G. 1929. Salmon Tagging Experiments in Alaska, 1927 and 1928. *Bull. U. S. Bur. Fish.*, 45: 1–23.

RICH, W. H., AND SUOMELA, A. J. 1927. Salmon Tagging Experiments in Alaska, 1926. *Bull. U. S. Bur. Fish.*, 43 (II): 71–104.

SAMAAN, A., AND STELLA, G. 1935. The Response of the Chemical Receptors of the Carotid Sinus to the Tension of CO_2 in the Arterial Blood in the Cat. *J. Physiol.*, 85: 309–319.

SCHMIDT, C. F. 1932. Carotid Sinus Reflexes to the Respiratory Center. I. Identification. *Amer. J. Physiol.*, 102: 94–118.

SHELFORD, V. E., AND POWERS, E. B. 1915. An Experimental Study of the Movements of Herring and Other Marine Fishes. *Biol. Bull.*, 28: 315–334.

SMYTH, D. H. 1937. The Study of the Carotid Sinus Respiratory Reflexes by Means of Chronic Experiments. *J. Physiol.*, 88: 425–435.

WARD, H. B. 1921. Some of the Factors Controlling the Migration and Spawning of the Alaska Red Salmon. *Ecology*, 2: 233–254.

————. 1927. The Influence of a Power Dam in Modifying Conditions Affecting the Migration of Salmon. *Proc. Nat. Acad. Sci.*, 13: 827–833.

————. 1929. Further Studies on the Influence of a Power Dam in Modifying Conditions Affecting the Migration of the Salmon. *Proc. Nat. Acad. Sci.*, 15: 56–62.

————. 1930. Some Responses of Sockeye Salmon to Environmental Influence During Fresh Water Migration. *Ann. Mag. Nat. Hist., Series* 10, 6: 18–36.

————. 1932. The Origin of the Landlocked Habit in Salmon. *Proc. Nat. Acad. Sci.*, 18: 569–580.

WILLIAMSON, H. C. 1927. Pacific Salmon Migration: Reports on the Tagging Operations in 1925. *Contr. Canad. Biol. Fish.*, 3, No. 9.

WILLIAMSON, H. C., AND CLEMENS, W. A. 1929. Pacific Salmon Migration: Report on the Tagging Operations in 1926, with Additional Returns from the Operations of 1925. *Contr. Canad. Biol. Fish.*, 4, No. 29.

————. 1932. Pacific Salmon Migration: The Tagging Operations at Quatsino and Kyuquot in 1927 with Additional Returns from the Operations of 1925 and 1926. *Biol. Board Can., Bull.* 26: 1–16.

CONFERENCE ON SALMON PROBLEMS

Those who participated in the symposium and others interested met for further discussions on Thursday, June 30, 1938, under the auspices of the Fisheries Research Board of Canada in the office of the Secretary, Mr. J. J. Cowie, who acted as Chairman. The following is an edited report of these discussions:

Separate Biological Races

Mr. W. J. M. Menzies presented the following paper:

The existence of separate types of salmon in individual rivers is too well known to require either emphasis or proof. In some rivers the run may commence in the late autumn and winter months (Rhine, Vistula, Tay, Spey). In others it may not commence until the spring (Beauly, Ythan, Laxford) and in yet others the run may be confined to the summer months (most west of Scotland rivers). In some rivers the fish may be predominantly large; in others grilse may form the greater part of the catch. Such variations might suggest special local stocks, but at the same time they may equally well be explained by some particular quality in each river which induces, or entices, a run of a certain type of fish at particular seasons of the year.

Beyond these elementary facts, however, certain other evidence with a more direct bearing may be found. For instance, the size of a river or the type of its mouth has no direct relationship to the number of fish which enter it. The Tay, with a wide open estuary and a considerable body of water, has a run of salmon very many times larger than the Forth, which has an even wider open estuary, separated from the Tay by only a narrow spit of land, and a water flow which, although smaller than that of the Tay, is considerable. Similarly the Ythan has a very much larger run of salmon than the Ugie, although both are of the same type and not markedly different in size. Other instances could be quoted.

If each river did not have a local stock then the limitation of netting in any particular waterway would not be reflected in later years by an increase in the number of fish in that river. And yet we have the much quoted and well authenticated cases of the Aberdeenshire Dee in former years and the Wye in this century where the stock has been built up from a very low to a very high level by the severe limitation of netting within the river. The increase has not been merely an increase in the stock of fish by reason of the number which escape being netted, but has been an increase from year to year as the progeny of the successively larger spawning stock have had time to develop and return. Ultimately in both cases the stock has so increased that the limited number of nets catch more fish than did formerly a very much larger number of nets. A similar case exists and has been authenticated by definite figures in the Conon where restriction took the form of allowing a fixed engine (a cruive) in the river to remain unfished. A corresponding improvement is at present being brought about in the Ness where for 15 years nets at the mouth of the river have been allowed to remain unworked.

Evidence of the same type suggests that a local stock must also exist even in the tributaries of at least the larger rivers. In the Aberdeenshire Dee for instance certain tributaries with good spawning ground have a large stock of fish, others with poorer spawning ground have fewer, and up two other tributaries, which are of considerable size and with the same quality of water as many others, very few fish indeed go. Both these tributaries have impassable obstructions only a mile or so from the mouth and only a very limited amount of spawning ground exists below these falls. Did salmon enter the tributaries by chance, then as many should go up these last two as go up any of the other streams. When making a special inspection of the waterways in one of the Scottish outer islands

with a view to elucidating certain apparently anomalous sea trout fisheries I was much struck by the fact that all the waters which had suitable spawning ground were inhabited by sea trout while all those which were locally reputed to be devoid of sea trout had no suitable spawning ground for the fish.

Apart from these observational data we have also evidence from the fish themselves. In the course of body lengths calculated from the scales we have found that each individual river has a different average length of the smolts at migration and that the type of parr scale growth as well as the smolt age differs considerably from river to river. Differences in length, average age and type of growth are not necessarily connected with different parts of the country but may occur in adjacent rivers, *e.g.,* the Aberdeen Dee and Don are only a few miles apart and yet the parr differ so greatly in type that occasionally among fish caught in the Dee one may occur with a scale growth so different from the average and so like that of the Don as to suggest that it is a chance wanderer. A comparison of the weight to length ratio of salmon from different rivers, when all are caught just fresh from the sea, also shows that each river has a certain class of either relatively fat or comparatively long and thin fish. This particular feature can be traced not merely for the whole stock but for each sex and each year class individually just as the average smolt length and the type of parr scale growth is found to vary not merely for the whole catch but also when each age class from different rivers is compared by itself.

One final essential difference between different rivers has to be referred to before the situation is summed up. It is that at the same times and with the same age groups of salmon those of one river may have an average length and an average weight which are both greater than the corresponding details for the other river.

It is true that even if specific local stocks for individual rivers do exist we cannot expect that the distribution will be absolutely perfect and that a few fish will not occasionally enter, possibly temporarily, a wrong river. But if we can quote as between different rivers and in strictly comparable circumstance differences of weight, length, condition (ratio of weight to length), distribution of age groups, smolt lengths and ages, and types of parr growth, then I do submit that the only explanation can be the existence of separate biological units in each river which through course of time and in response to the local environment have developed these characteristics. When such features are reinforced by more equivocal circumstances such as the variations in the times of run and in the proportions of different age classes as well as the total number of salmon in each river any other conclusion seems to be impossible.

The development of the special scale characteristics can also be used to check the migrations of salmon marked in the sea and to ascertain if those which make long migrations from the place of marking to a river have done so by chance or with a definite destination in view. In all cases which I have tried, the test has shown that the fish are of a type which belongs to the particular area or the particular river where they were finally found. For instance in the scale of a salmon which was marked on the Scottish northwest coast and which was recaptured on the Norwegian coast, Professor Dahl agrees with me that the parr scale is typical of that of a Norwegian west coast river; it is certainly quite unlike that of any Scottish river. On the other hand the Forth salmon have a particularly typical parr growth which shows on the scale a small first year and a good second year. Let us consider the scale of a salmon marked in Norway and recaptured in the Forth and that of another marked at Loch Inchard and again taken in the Forth. The first scale practically duplicates the growth of the type scale and although the second is not so clearly marked the calculated lengths obtained from it are of the same order. Finally parr growth and consequently scale growth in the Tweed is exceptionally good and there are concurrently a considerably

higher proportion of one-year smolts than in any other Scottish river. A typical one-year-old Tweed smolt scale was taken from a grilse marked in Norway and recaptured above the tidal waters of the Tweed. A typical two-year-old Tweed parr scale was taken from a fish marked at Loch Inchard and killed later in the Tweed.

Yet another method of checking roughly the movement of at least the grilse in the Scottish experiments is afforded by the fact that the grilse of the west coast rivers are slightly longer at the end of their first sea year, and slightly longer and heavier at the end of their feeding period, than are the grilse of the east coast rivers. I have taken out these figures for the grilse which were marked on the northwest coast in 1936 and 1937:

Recaptured	Length first sea year		Total length and weight			
	1936	1937	1936	1937	1936	1937
	cm.	cm.	cm.	cm.	lb.	lb.
East coast	49.	43.5	63.	57.5	5.5	4.2
West coast	50.	46.5	67.	65.5	6.6	5.5

These figures show conclusively and consistently that the marked fish conformed to the results obtained from fish which have actually returned to, and been caught in, rivers of the two coasts. I should perhaps explain that the considerable difference between the corresponding figures of the two years was due to the fact that the grilse of 1936 were exceptionally well grown everywhere and were approximately one pound above their average weight.

Dr. Huntsman. We should define local stocks. From Mr. Menzies' presentation and from previous discussions with Dr. Rich it would seem that there is no point at issue. Dr. Rich stated that he referred not necessarily to anything more than local populations.

Mr. Menzies. We should get a satisfactory name for a local stock in an individual river—I have called them separate biological races.

Dr. Huntsman. I believe it desirable to have some definite way of indicating that there is no necessary implication of heredity.

Mr. Menzies. We have two different things—stock in a river and spring fish, summer fish or grilse.

After discussion of the suitability of "race," "stock" and "population" it was generally agreed that "stock" would be desirable.

Dr. Huntsman. There will be hereditary units. Will it be worth while finding out when and where any such are shown for two generations?

Mr. Menzies. By hereditary units you mean fish which would return to their native river however you treated them.

Dr. Belding. Can anyone present furnish any evidence of hereditary factors in the different river stocks?

Mr. Menzies. No.

Sea Habitat of Salmon

Dr. Belding introduced this subject, calling attention to the occasional observations of post-smolt salmon.

Dr. Huntsman. In the Gaspé Basin there have been records where post-smolts have been taken by the fishermen, weighing about three-quarters of a pound. Kendall reports that not infrequently they are taken in traps on the New England coast.

Mr. Menzies. Is there no possibility of confusing the young salmon with your migratory trout?

Dr. Belding. No. At all seasons of the year in Massachusetts Bay and on the fishing banks, such as Georges, miscellaneous salmon are taken by the trawlers. The records indicate that the salmon are taken within a depth of 70 fathoms. In the old days on Cape Cod traps have taken salmon even in January. These records undoubtedly constitute a small percentage of the total catch of salmon, since most captures have not been reported. Dr. W. C. Kendall has made a collection of these reports from various sources, such as newspapers, and fishing returns. Evidently scattered salmon are found off the New England coast at all seasons of the year.

Dr. Harold Thompson, formerly of Newfoundland, believes that the salmon frequent the offshore slopes to the east and southeast of Newfoundland or possibly further south. His opinion is based upon the difference in the time of arrival and the local characteristics of the salmon in the several sections of the east coast of Newfoundland. The time of arrival is about two weeks later in Labrador than in southeast Newfoundland. Also there are certain differential characteristics, particularly in the length of the smolt life (river years) between the salmon of the various sections of the east coast of Newfoundland. Dr. Thompson believes that the salmon of these several areas came from special divisions of the slopes off Newfoundland.

There is no evidence as to the exact ocean habitat of the Gulf of St. Lawrence salmon. It is possible that they may remain entirely within the Gulf, as Dr. Huntsman believes. My personal point of view is that the majority go beyond the confines of the Gulf of St. Lawrence.

My interpretation of the 1937 Port-aux-Basques tagging operations is that the salmon of this locality probably come from outside and are passing through Cabot Strait. It is possible that they may come to Port-aux-Basques from within the Gulf of St. Lawrence and then redistribute themselves or that they may even be in the vicinity of Port-aux-Basques and not reach the drift-net fishing area until a particular time. I am convinced that Port-aux-Basques is a way station, and that the salmon do not remain there as they do in the Miramichi drift-net fishing area. There have been only four recaptures of tagged salmon in the Port-aux-Basques drift-net fishing area, all within three days after tagging whereas in the Miramichi drift-net fishery area recaptures have been evenly distributed over a period of five to six weeks.

The transitory nature of the Port-aux-Basques salmon and the isolated captures of salmon at all seasons of the year off the coast suggest an ocean habitat beyond the borders of the Gulf of St. Lawrence, but no definite evidence is available. We know something about their onshore movements within the Gulf of St. Lawrence. The fish first appear at Port-aux-Basques shortly after the first of May, about three weeks earlier than their arrival on the western shores of the Gulf.

No information indicating that there is an oceanic mixture of the European salmon and the American salmon is at hand. The little evidence which I have collected is entirely against this idea. There are annual fluctuations in the average weight of the salmon, probably due to feeding conditions in the ocean. The fluctuations are similar for the salmon of the Moisie, Godbout, Restigouche and Cascapedia rivers over a period of many years. The fluctuations in the salmon of the Wye River (England) do not agree at all with those of the American salmon. This fact suggests that the salmon of the Gulf of St. Lawrence have a different oceanic feeding ground than have the salmon of England, and that there is no mingling of the salmon from the two sides of the Atlantic.

Dr. Huntsman. We have facts similar to those Dr. Belding has given; and perhaps as a result of a different approach we come to different conclusions to those he has indicated. Let us take the view that salmon come in from the ocean, have a feeding ground outside. Undoubtedly a large amount of food is available in the inside waters, *e.g.*, the Bay of Fundy. For the Bay of Fundy the evidence is against the idea that the salmon come in from the ocean. Salmon are rare at Grand Manan at the mouth of the Bay on the New Brunswick side. On the opposite side of the Bay at Brier Island I was able to get only one record of a salmon being taken. When it comes to the order of appearance of the fish related to the St. John River, for example, if they were coming from outside, you would expect that they would be caught first at the outer end of the fishing area whereas the exact opposite is the case. They get them first next or in the harbor. At the head of the Bay of Fundy they are taken in weirs along the south shore of Minas Channel, and they are actually caught first at the inner

end of the stretch of coast where the fishery is conducted roughly a month earlier at Cape Split, the inner end, than at Margaretville, the outer end.

On examining the facts of the time of appearance of the salmon on the Canadian Atlantic Coast, I have failed to find that they correspond with the idea of progressive movement from the ocean to the rivers, but I have found a relation between the time of the salmon's appearance and temperature. Where the fishery starts is the place where the water warms first.

When we enquire whether or not the fish are feeding locally when they are captured, we get definite information from the fishermen of food being obtained in the salmon in these localities and this we have been able to verify. Also the salmon are taken occasionally in the various types of gear that might be expected to secure them, such as long lines (trawls) or hand lines, or shore weirs, so that we see only evidence indicating that they are remaining locally, feeding, growing, and remaining relatively inactive during the winter. They start to become active when the water warms up in the spring and are to be caught when moving about.

The gear by which they are ordinarily caught is such as to capture them effectively only when they cease feeding and roam about actively or when concentrated near the shore or near the surface, and so run into the nets that are moving with the water near the surface. The whole picture fits in with the salmon occurring in the regions in variable proximity to the mouths of the rivers.

Mr. Cowie. That is in the Bay of Fundy.

Dr. Huntsman. It applies also to the Gulf.

Dr. Belding. My remarks referred to the salmon of the Gulf of St. Lawrence. I consider that entirely different conditions exist in the St. John River and the Bay of Fundy sections and still more different in the small rivers of the Minas Basin section. I believe that when the salmon stock of a river consists chiefly or entirely of grilse that these salmon do not go far from the rivers. For instance, in certain rivers of Newfoundland, which are frequented only by grilse, the fish are much smaller than in other sections, a fact which may be explained by the assumption that the salmon do not go far from the river influence and are subject to a local environment.

Dr. Rich. Why do they mature only as grilse?

Dr. Belding. In these grilse rivers the only spawning salmon are the male and female grilse.

Dr. Huntsman. It is desirable to consider the various possible interpretations of the facts, so that the truth may be reached. It would be expected that some of the Port-aux-Basques fish would be from the rivers of the southern part of the Gulf of St. Lawrence. The young may well be carried out to the ocean and may also be carried back and concentrated at that point. It being a place where there is practically no river influence, the salmon there on ceasing to feed would roam widely and far and not quiet down until they reached river influences. In concluding that the salmon remain largely in the vicinity of the river mouths, I have extended sea distribution of part of the stock clearly in mind. We have definite evidence that Bay of Fundy fish have been caught on the east coast of Newfoundland.

Dr. Belding. In general the Port-aux-Basques salmon differ in their characteristics from those of the west coast of Cape Breton, as shown by Dr. Huntsman's scale readings of the Margaree fish. Therefore there would not be any great number of the Port-aux-Basques fish passing to Cape Breton.

Dr. Huntsman. There is evidence that Miramichi kelts go out into the ocean and reach the east coast of Newfoundland. There is perhaps a greater likelihood that some of the smolts take such a course.

Dr. Belding. The introduction of kelt, which possibly react differently, into a discussion on maiden salmon tends to confuse the picture.

Mr. Menzies. Is it possible for them to be carried back at the rate of 28 miles a day,

from the Port-aux-Basques area into the Gulf?

Dr. Belding. That was the maximum rate in the 1937 tagging experiment.

Mr. Menzies. If they are carried back they are only carried back by the residual current. If they are carried up so far on the flood tide they will be carried back part of the distance on the ebb. Can they be carried 28 miles a day on one residual?

Dr. Huntsman. Only a part of the salmon show such a rate. With salmon moving actively and at random great varieties in rate would be expected, and the effect of the current would be shown only in the average rate.

Mr. Menzies. There is directed swimming. You do go so far as to say they swim as well as are carried. They swim in a directed fashion. They may drift in one direction at 10 or 11 miles a day.

Dr. Belding. The average rate for all recaptured salmon was 12 miles per day.

Mr. Menzies. They will drift 15 miles a day in one direction. If their swimming is not directed, then you must surely admit they may be going in any direction.

Dr. Huntsman. For current it is not any direction but a certain direction. There are no facts as to how rapidly they could be carried in the current from Port-aux-Basques inwards. Their active movements may be directed to some extent but of that I have no evidence. They seem to be held in water from the rivers, which involves a certain amount of direction, they move to and fro, but do not leave it.

Dr. Belding. How do you explain the number of salmon taken in Casco Bay and along the coast of Maine? Greater numbers appear on the coast than go up the Penobscot, Denis and St. Croix rivers. Where do they belong?

Dr. Huntsman. I would have to have that demonstrated first, but some from the Bay of Fundy do go out towards Maine.

Mr. Menzies. One point Dr. Prefontaine raised regarding the Bay of Fundy, am I not right in saying fish are caught earlier near Cape Split, earlier than at St. John and later caught out toward the mouth of Digby Gut? In the earlier period is the river level higher than in the later?

Dr. Huntsman. There is no river—just small brooks.

Mr. Menzies. That is right away from the actual river estuary.

Dr. Huntsman. There is a gap between that fishery and the river estuaries.

Mr. Cowie. The temperature would be higher at the head of the Bay.

Dr. Huntsman. Yes. The fish are earlier owing to the temperature.

Mr. Menzies. We have no facts on which we can make the wildest assumption as to where the salmon are in the sea. Salmon are caught at sea but there is quite a bit of trouble getting records. Fishery people collect them for us. We also paid three shillings for all these small salmon-like fish caught in herring nets. They were all trout and no sign of a salmon. There are a few cases of salmon being caught 30 or 40 miles off the coast. So far as Scotland is concerned we are not going to attempt to find out where they go outside territorial waters. I am safe to say that if we can find out where they feed and the routes they take coming back it might be dangerous to the whole of our fishery.

Dr. Rich. On the Pacific coast the silver and Chinook salmon are taken all along the coast, within 30 or 40 miles of shore, (chiefly fairly close to shore) and a great many of the fish will not mature in the year in which they are taken. Some seasons of the year more than half are immature. Red or sockeye salmon are not taken during their sea life at all. There are two interesting observations in regard to the red salmon that have never been recorded; they are, perhaps not of a nature that should be officially recorded. Dr. W. F. Thompson of the International Fisheries Commission reported to me a number of years ago that during his experiments in the halibut work a single red salmon was picked up somewhere in the middle of the night out in the middle of the North Pacific, about half-way between Kodiak and the Strait of Juan de Fuca. I have seen the specimen and have examined scales from it, an adult red

salmon. It must have been seven or eight hundred miles offshore.

Then a young man who had been in fishery work but was, at the time, an officer on a boat sailing to the Orient, stated to me that he once saw a school of red salmon several hundred miles offshore. Fishermen who are used to observing salmon at sea can tell the species by the way they break water.

Sockeye are feeding in many places the year around. Just south of the Alaska Peninsula most of the red salmon are feeding.

Behavior of Salmon in the Sea

Mr. Menzies. On the European side, including even the Baltic, there are two sets of circumstances. The fish follow two entirely different sets of conditions, one set when they are on their main migration coming to the coast, another set when they have approached comparatively close, say to within 50 miles of the river they are going up. So far as we see, after they have gone more or less directly to within 40 or 50 (usually 20 or 30) miles of the river they will ascend, they then go straight upstream if the conditions of the river are suitable. I have some evidence about that. When the river conditions are not such as to tempt them upstream then they hang about the coast.

In the migrations within 40 or 50 miles, they do respond undoubtedly to certain local conditions. They either go to the lee shore or they will go down wind along the coast. If the wind is blowing on to the shore they will come quite close; proved beyond a doubt by the catch of salmon along the shore. If the wind is offshore they move away from the coast. If the flood tide is running east they run east. On the ebb tide they will come back west, and that movement is more than merely drifting with the tide; especially from the last week of June until August. They are moving at a faster rate than the rate the oceanographers say the tide is moving.

Mr. Cowie. The movement is with the tide.

Mr. Menzies. But at a greater rate than the tide. They do not go parallel with the shore, they move off and on. And they must move off and on because in certain parts of the east coast of Scotland bag-nets extend for a half mile into the sea.

In a certain bay there are ranges of eight bag-nets, each bag-net 100 yards long, set with 100 or 150 yards between each. These nets fish approximately equally well. Occasionally you will get one inshore net better than some of the others. If the fish did not move off and onshore it would be impossible for a bay to be fished like that and to pay for the gear.

Dr. Belding. Do the outer or in the inner nets catch the greater number of salmon?

Mr. Menzies. The outer one may catch the same as any of the others.

Dr. Belding. In the Bay Chaleur the nets near the shore usually catch the greater number of salmon, but the reverse may occur in certain localities.

Dr. Huntsman. In trying to apply his ideas to our conditions, I am not quite clear as to how Mr. Menzies distinguished between the two behaviors. How do you know when the salmon are approaching the coast or the river on their directed "main migration" and when going away from as well as toward it in undirected local movements?

Mr. Menzies. I do not say anything about going away, when they are not on their main migration. By correlating the fishing experience with the marking experience we know.

Dr. Huntsman. Is it that in marking at a certain place you get fish which subsequent facts of recapture show are there for some time? Then you must have both types of behavior there together. Certain fish caught at a place behave differently from other fish caught at the same place.

Mr. Menzies. You get a certain proportion of fish recaptured at the place of marking after two or three weeks.

Dr. Huntsman. Then the differentiation between the two behaviors is based upon where the fish are recaptured, not

upon what the fish are, that is whether or not they are in the vicinity of their rivers.

Mr. Menzies. The marking results quite clearly show that at the north end of Moray Firth and at Thurso Bay we are dealing with fish belonging to the locality.

Dr. Huntsman. That illustration is more clear cut. Of the fish caught subsequently none were any distance away. The outstanding behavior at Port-aux-Basques which Dr. Belding describes so well was the reverse; the fish were noteworthy in not staying there any length of time.

Mr. Menzies. They are on their main migration?

Dr. Huntsman. Does that mean that they were on the way to some distant place which is the home stream?

Mr. Menzies. What do you call "distant?"

Dr. Huntsman. Some of the fish tagged at Port-aux-Basques went only a few miles before being recaptured.

Mr. Menzies. Migrating closer and closer to the river mouth. They were not local fish. Distance does not come in.

Dr. Huntsman. They were away from river influence.

Mr. Menzies. That is where I differ from you. When I mark a fish in Scotland within a quarter of a mile of a river it may be away from the river influence.

Dr. Huntsman. At the head of Bedford Basin inside Halifax harbor, there is the Sackville River, on which there is a hatchery where the local fish are trapped for hatchery purposes. The fish are taken by fishermen in the upper end of that basin which forms an estuary for the river. In one season which was extremely dry, the local people report that while fish could be caught for a time, later they left the locality, presumably with failure of the river influence.

Mr. Menzies. You said from the fact that they were there steadily that was their river. Later it showed, when they left, that was not their river.

Dr. Huntsman. How can I accept that assumption?

Mr. Menzies. Large numbers went up the local rivers, they captured the marked fish.

Dr. Huntsman. Do they belong to a local river if they are four or five miles up, sufficiently far up?

Mr. J. A. Rodd. Those fish were apparently on the way to the spawning grounds. It was quite late in the season when they left. Apparently they were near the spawning grounds.

Dr. Huntsman. The point I wish to make is that they left. They did not go up the river, although they had been quite visible in the outer bay. They exhibit a different behavior when near the spawning beds.

I am having great difficulty in getting from recaptures any clear evidence of a relation between the behavior of the fish and their nearness to the rivers from which they have come. There is definite evidence of movement to other rivers.

Mr. Menzies. That is the exception to the rule.

Mr. Rodd. Before the fishway was put in at St. George, New Brunswick, the fish could not get over the falls, they would go to the St. John River. They were not caught there. You could see them from the falls. The tides come to the foot of the falls.

Mr. Menzies. In dry weather they go from one estuary to another and this difference shows it.

Dr. Huntsman. It is clear that we have comparable conditions on the two sides of the Atlantic and that the behavior of the salmon is similar.

Mr. Menzies. But we have nothing comparable to your facts of feeding salmon in the estuary such as you have in the St. John.

Mr. Cowie. When I was over in the Old Country 10 or 12 years ago, I found that the late Duke of Richmond and Gordon had a small hatchery near Gordon Castle on the Spey, about 12 miles from my old home. On visiting the hatchery I found that there were a million salmon fry in it. I asked the man in charge where they got their eggs from which the fry had been developed, and I was rather astonished when he told me that they simply salvaged the eggs from fish at

the mouth of the river about five miles below the hatchery. These fish evidently had not been able to go up the river to the usual spawning places but milled around the small estuary, consequently the eggs were taken from the fish there; otherwise, as I was told, the eggs would be entirely lost.

Mr. Menzies. We marked all the fish they caught. Fish spawn there late in the season (November and December). For several years we marked them there. The hatchery is now closed. The fish were actually caught in the river from the top of tide to about five miles upstream.

Dr. Belding. The Moisie River is quite a large river. At one time a landslide caused a marked increase in the turbidity of the water at the time the salmon were running. All of a sudden in the estuary of the small neighboring Matamek River there appeared an enormous number of salmon. These salmon remained there for a few days and then disappeared as rapidly as they came

Dr. Huntsman. The point at issue can be settled only by actually knowing the origin of the fish. Some stay in the locality and some go elsewhere.

Mr. Menzies. You can say that because they go there and we find they belong there.

Dr. Huntsman. If you want to have it clear-cut, the fish should be marked as smolts and their behavior ascertained when they are taken in the sea, and tagged and liberated there. Circumstantial evidence, susceptible to different interpretations, does not seem to me to be satisfactory.

In this matter of sea behavior ("main migration") and local behavior, it seems to me to be of significance as to whether the salmon can be caught in drift-nets or in shore gear. There appears to be a change in this respect when a spate comes along. For the St. John River salmon show such a difference as between those in the zone of river influence and those just outside the zone. Also the drift-nets when in the outer part of the zone have the fish meshed entering chiefly from the outside, when in the middle of the zone from both sides equally, and when in the inner part of the zone from the inside chiefly. Also, the fishermen at the river mouth state that they can catch the salmon when the spate is on, but when it is passing off the fish go past them into the river.

Behavior of Salmon in the River

Mr. Menzies. The majority of our rivers run straight out on to the coast. Tide water does not remain in the estuary; when the tidal water runs out there is only river water. The Tay, however, is a very good example of a river with a large estuary. It is our biggest river. The fish pass into the estuary and then they are going up and down with the tide in the estuarial part.

I have a complete record of the catch of fish in a certain river. The estuary is about eight miles long—the fish go up and down. We have a very complete engineering record of the water flow in the river and the actual number of fish caught each day. In that estuary there is a net fishery at the mouth and one about one-half way up. At the top of the tide there is a set of traps right across the river—fish caught in these traps had definitely left the tidal water. I have been able to correlate the average flow of that river. I have averaged the flow for each of the months of May, June and July, then I have also taken the total number of fish caught in the nets lower down in the estuary and I have worked out the percentage that were caught in each month in the fishing weirs. These last fish were actually on their way upstream. The graphs show (1) the average height of the water and (2) the percentage caught in the cribs or weirs. The curves in illustration follow one another. The correlation is extraordinary. The correlation simply bears out what I have said as to the behavior of the fish.

Dr. Huntsman. It is the same for the Margaree.

Mr. Menzies. The correlation to me is perfectly clear. If you get a spate at the end of June it is carried over into July and may give July a higher water flow than belongs to it. It may be very low from July 7 onwards.

Dr. Rich. Did you ever try correlating with the rise of water?

Mr. Menzies. Yes. That depends upon

the type of flood. If you get a medium or small flood with a clearing between, up will go the fish. Say a month or six weeks dry weather and the river water gets foul with algae. It comes down foul and the fish will really not start to run until the water is clear. Rainfall is not nearly as good as water volume. The water may not go into the river if the weather has been dry.

Dr. Belding. The first stage of onshore migration is when the salmon approach the coast. Some fish may enter rivers near the point of appearance while others may move along the coast for hundreds of miles, their distribution becoming successively more and more localized.

At times salmon, such as the fish originally tagged at Port-aux-Basques and recaptured in Labrador, do not appear to conform to the general distribution of their fellow salmon.

In the Miramichi drift-net fishery tagging we found a fairly wide spread but nevertheless a localized range, confined to the east coast of New Brunswick and the Bay of Chaleur. In the case of the tagging at Grand Greve, Gaspé, the distribution was of the same general type as obtained by Dr. Huntsman at Margaree Harbor, in that the salmon spread in both directions along the coast with a noticeably local range. In other words, coastal tagging shows distribution at the particular point and laterally in either direction.

Mr. Menzies. They might possibly go back and be caught in their own river—fish within 50 miles of the river of their destination.

Dr. Huntsman. The behavior just described by Dr. Belding for the Margaree, Miramichi and Gaspé districts is, in contrast with that at Port-aux-Basques, related to river influence, that of the St. Lawrence River, whose water passes out along the southern side of the Gulf of St. Lawrence. Along this side the salmon after liberation spread, but stay in the St. Lawrence influence.

Dr. G. Prefontaine. For the St. Paul River near the Strait of Belle Isle in 1937, salmon tagged up the river went out and lower down. They were captured moving out.

Mr. Menzies. When was the tagging done?

Dr. Prefontaine. In June.

Mr. Menzies. The movement was back and forth as in your description.

Dr. Belding. We have coined the term "pocketing" to designate the effect of conditions such as in St. George Bay in Newfoundland, where the number of recaptures is far in excess of the commercial catch. It appears that the salmon from Port-aux-Basques remain for some time in this area, which because of its physical characteristics may act as a way station for salmon ultimately bound elsewhere.

Dr. Huntsman. This condition is comparable with that in Scott's Bay on the south side of Minas Channel, Bay of Fundy. There is the same pocketing of the salmon. But there is this difference, you have rivers emptying into Bay St. George, Newfoundland, but Scott's Bay in Minas Channel has no rivers.

Dr. Ward. This conference has brought out, more distinctly than was evident in my previous communications, the fact that I have been working along a very different line from others who have spoken. I have stayed away from salt water. I have spent all of the time devoted particularly to my own observations and experiments studying the live fish after they were definitely in brackish water.

I have been interested to determine environmental factors that influence the movements of the fish and my conclusions do not agree with the views held by many distinguished friends of mine.

I believe that the fish are determined in their movements by the environmental conditions; in other words, their movements are conditioned movements. Among adult salmon having embarked upon their course in fresh water we have to deal with problems that involve a more limited range of choice in movements than is presented in ocean waters. My observations have been principally directed to the Pacific salmon, and especially to the sockeye salmon which

I studied first in the Skagit River in Washington.

Environmental conditions are clear in such a stream; one finds the fish subject to a few clearly evident stimuli which guide the majority of their actions. The stimulus which is most distinct is mechanical, the current influence. The original study of Rutter on the movements of salmon through estuaries, dealt with the adult red salmon or sockeye. One recognizes that in estuaries the influence of the tide twice a day is at one period concurrent with the stream influence and at the other period antagonistic to the river influence. Rutter observed what I think has been seen since then by numerous others that the fish go up with the falling tide and turn out with the inflowing current. With each tide they go further up and a less distance down the estuary so that each tidal movement is up and back part way which ultimately carries them up stream beyond the tidal influence. During this period one sees them milling around at the turn of each tide when they are observed in the eddies where the fish actually act as if uncertain where they were going. I have been much impressed by the uncertainty of their movements at that point.

The influence of a current stimulus is also demonstrated in their movements in fresh water. So long as they are in contact with a single current where the river is flowing steadily without contributions from side streams, they merely keep on moving. To be sure in a river they do not move constantly throughout the full 20 hours, but in warm weather at least they rest in deep pools during the periods of bright daylight. They also move little at night, but start up conspicuously in the early hours of morning twilight and go on upstream against the current.

In any large river it is difficult to observe movements of the fish in the stream generally. One can see the salmon only at special places as they pass over shallows or barriers. In this way I have found that the salmon apparently rest at night since they did not use a fishway at all during the hours of darkness even though this fishway was experimentally illuminated brilliantly at night, during part of the period of migration.

The influence of light on upstream migration of adults was illustrated in striking fashion by my observations at the Rock Island dam on the Columbia. Local fishermen had reported that salmon did not use the ladder which was well located and well constructed. I started my observations at the dam early in the day, indeed soon after dawn and found the fish at that hour going vigorously up the ladder and into the river above the dam. The ladder is located at the east bank where mountains almost at the margin of the river shelter the water from direct rays of the morning sun. The fish kept running up the ladder in good numbers and without the least hesitation until the sun's rays coming over the ridge struck the water in the ladder. Then the salmon run stopped almost immediately and not a single salmon entered the box at the foot of the ladder during the day time. Movements in the afternoon began late, apparently when the rays from the sun in the far west were so oblique that the light was totally reflected from the surface of the water and when indirect illumination was also reduced. Salmon entering the ladder came out of deep water and on leaving went down into deep water.

The only place you could usually see the salmon was in the ladder. The compartments in the ladder were very large and the space was generous; they went through the boxes like a college hurdler, loping over the weirs with perfect ease and then turning like a flash at the top compartment and disappearing through the gate into the river. I have made all sorts of efforts to follow the fish consistently in that river, above and below that dam, but without success. They appear now and then finning at the surface, but one cannot follow constantly a particular fish.

The same activity is shown on the Skagit River, a much smaller stream where you can see them clearly and follow them. They move perfectly definitely up stream until

they come to the place where the Baker River, a major tributary, joins the river. There there is an eddy in which they mill around for a variable time depending upon the definiteness of the current from the Baker. But all of the sockeye turn into the Baker instead of following up the Skagit, although the angle between the two streams is reentrant and they have to turn in somewhat the opposite direction from their previous course. In larger eddies not at stream junctions salmon often mill around, heading into the current of the eddy and leaving it apparently when drawn into contact with stronger downstream currents at the margin of the eddy.

Now, after studying the situation at the junction of the Skagit and Baker as to chemical, physical and other differences between the two streams, I demonstrated a constant and consistent difference between the two streams at the time of the sockeye migration of something like two degrees Fahrenheit. To leave no question as to the consistency and accuracy of the temperature records, two recording instruments were placed just above the junction where the streams are perfectly free of possible connection, and yet so near as to show conditions where the waters mingled; records were obtained for 24 hours per day throughout the entire period. Some fluctuations in the stream are observable due to warm days, melting snow or ice in glaciers from the mountains which drain into the two streams. But these temperature fluctuations are slight and preserved that consistent relation noted until about mid-September, when strikingly enough the condition was reversed and after that the temperature on the Skagit River was steadily lower than on the Baker. There is a small sockeye run in the fall and those fish were caught above the junction of the Baker and in the Skagit.

Attention must be directed to a change which was brought about by the installation of a hydro-electric plant, a mile above the junction of the two rivers, and a dam by which was formed a lake eleven miles long. Temperatures in that body of water became considerably altered. The surface temperature was very much higher than the water had ever been in the canyon previously. The river was fed by water taken out for the plant and the temperature in the tailrace was lower than ever before; subsequent to the construction of the dam the temperature was four degrees lower in the Baker than in the Skagit but the choice of the salmon for the Baker River was not modified by a drop of that extent.

Going to a point a little higher up on the Baker, I found a remarkable example of the effect of the quality of the water. At a point before you reach Baker Lake Sulphur Creek runs into Baker River; it was fed by springs and melting snow on the side of Mount Baker, and was distinctly colder than the river itself. But the creek water was highly impregnated with sulphur.

Some years ago the fish went right past that cold water and that seemed to contradict my views with relation to temperature influences. I had the opportunity of testing the effect later. At a time some ten years after I started my observations, Sulphur Creek was diverted from its course well up on the mountain. The water from the lava fields impregnated with sulphur was turned into another stream which fed a commercial power plant. After that Sulphur Creek was fed exclusively by large springs below the lava and the water was clear, cold and pure.

I visited the place by routine two years after this change was made. I found to my astonishment that sockeye were entering Sulphur Creek and were attempting to go up in considerable numbers. I studied the stream continuously and found that until a time some two weeks later when the volume of that stream became very small, the fish scrambled up as far as they could or until they reached a long rapids which large fish could not ascend. Later they came up into small bays below these rapids, swimming around and trying to make the ascent; ultimately as the water fell still further they went back to the Baker River and up to Baker Lake.

The quality of the water that I have regarded as a chemical factor, I believe influ-

enced the action of these fish. The sulphur affects the fish apparently disagreeably. When the water became pure and clear and had no sulphur taste, then the sockeye entered and tried their best to utilize that stream as a spawning ground or as an access to a lake spawning ground which did not exist.

Another temperature influence may be well illustrated by observations on Baker Lake and lakes well up on the Copper River in Alaska, in both of which places the spawning grounds chosen were exclusively in spring-fed gravel found only at certain points in the lake. One could go round the lake with a thermometer in the water and by observation could determine that there was also an inflow of cold water at places where the fish were spawning and not at any other point, in those lakes at least. Selection of a spawning ground was specifically in spring-fed gravel with outflowing colder water.

I have said that the adult fish move constantly upward against the current. After hunting for many years I found an exception to that which is worth stating. Between the hydroelectric plant on the Baker and the dam is a stretch cut off by a fence from the river channel below the plant. Water flows down this stretch only when it is wasted from above the dam. On one occasion in the morning sockeye were found in the bay above the fence trying to get up the stream. They had gone under the fence and were working their way up the rapids to the dam. At a particular moment they stopped, evidently dissatisfied, and began suddenly to back off downstream. That moment was just when the flow of water over the dam stopped and the water level in the rapids began to drop rapidly. The fish stopped in the first deep pool they reached and then as the water became a little shallower they turned about and darted into the next deep pool, but stopped, again pointing upstream. As the water kept sinking they made another dash in the same way. Thus they were forced to continue until they got to the deep pools below the fence and only then stopped their downstream movement.

My work has been almost entirely devoted to observing the actual movements of the fish. I have studied the living fish days and weeks to see how they behaved and I have found no exceptions to these behaviors. I am convinced myself that there is no such thing as a mysterious influence as you call it. I believe the fish are guided by conditional reflexes.

Dr. Rich. Do you think that this conditioning can be accomplished in the early life of the fish and carried?

Dr. Ward. The conditioning can not be done in the early life of the individual fish. At the start of the period of sexual development the activity of the fish changes directly from one of seeking food to seeking conditions for reproduction.

Dr. Rich. The essential point at issue between Dr. Ward and myself has been whether or not the fish return to their parent tributary. There is a very large body of experimental evidence to which I referred yesterday, that supports the view that they do return. Anything that does not fit in with that theory and with the facts upon which the theory is based would have to stand a very careful scrutiny. I would ask for evidence contrary to that theory.

Dr. Ward. I am not dealing with the migrations in the sea, but I simply say that the fish carry out their activities under the influence of the environmental conditions.

Dr. Rich. The return of the fish is directed. Those of us who accept the home stream and the home tributary theory, only say that these environmental conditions are the guides that in some way direct the fish back. They go back. So far as the Pacific salmon are concerned I am thoroughly convinced that they do return to their home stream and home tributary, and any theory that does not fit in with that fact is open to suspicion.

Dr. Ward. A long time ago I asked in discussion: What do you mean by the home stream? If fish eggs are taken to a hatchery and hatched and the young fish are planted there, is that their home stream? Outside the Baker River, *i.e.,* in other branches of the Skagit River, which look like better spawning grounds than Baker

Lake, there have been by the Bureau of Fisheries something like 200,000,000 eggs and young planted within the last 30 years and the fish have never in any number come back to any stream except the Baker River. Do you refer to Birdsview as evidence of homing?

Dr. Rich. The fish run in there, and we counted them; there were many marked salmon in that tributary.

Dr. Ward. When the temperature was lower they went in there and made a run of salmon in that stream, but only when the water was colder than in the Skagit.

Dr. Rich. I think you will find that there are fish there every year.

Post-smolts and Condition Factor

Dr. Huntsman. The post-smolts about one pound in weight are captured regularly at the extremity of the St. John outflow at the time of the year (September) when presumably they have stopped feeding. Also, as Dr. Belding indicates, they are taken at the mouth of Gaspé Bay and in Minas Channel at the head of the Bay of Fundy. I am not certain of the time of year for Gaspé, but in Minas Channel they are taken at the end of the season only. The order in which the various sizes are taken is perhaps of significance. You have the fishery starting early in May with the very biggest salmon that have spent three years or more in the sea. These are replaced gradually by two-sea-year fish, then by grilse and finally by post-smolts. What is the significance of this order?

It is perhaps of importance that the gear, in which the salmon are captured in Minas Channel, consists of weirs which take all sizes down to post-smolts. This is unusual. It is somewhat similar for the St. John where weirs are fished around the outskirts of the St. John outflow. They take all sizes of salmon but very few of the large salmon. They do take very large numbers of post-smolts, but only late in the season in September. They seem to occur in as large numbers as could be expected in relation to the river. They must definitely live there to occur at that time of the year.

The interpretation of these facts, that I think is desirable, involves two points: First that the salmon are feeding there in the sea and that perhaps at the end of the season they stop feeding, roam about, reach shore and are captured in the weirs; second, it seems that under certain conditions at least the largest and fattest salmon cease feeding earliest in the season, then the grilse and finally the post-smolts. Capture in the weirs seems to represent the cessation of feeding. The larger they are, the fatter they are, and the earlier in the season they cease feeding. Post-smolts are not mature, so that this phenomenon is apart from sexual maturity.

Dr. Belding. On what do you base your figures, the length, weight, chemical examination of the tissues or the coefficient of condition?

Dr. Huntsman. The condition factor.

Dr. Belding. There are numerous factors which affect the condition factor or coefficient of condition. For instance, if in a series of salmon you calculate the condition factor from the average length and weight you get a different figure than if you take the mean of the condition factors of the individual fish. There are variations in the form of salmon and in the number of vertebrae that affect the coefficient of condition. I have found a difference as great as two vertebrae between the parr of certain rivers.

Mr. Menzies. The difference in condition is due to the vertebral count?

Dr. Huntsman. There are many complexities of course. Nevertheless this is merely a statement of fact and I find it correlated with the presumed cessation of feeding as shown by captures in the weirs. I put this up as a possible interpretation of the order observed.

Mr. Menzies. We do not seem to have the same order in Europe.

Dr. Huntsman. The condition described is not universal. If you ask the fishermen of the Margaree coast which come first, they say all kinds, no earlier capture of any particular size. In Minas Channel the condition is particularly well shown probably owing to the heavy tides mixing the water up thoroughly, all fish being exposed to the

same condition of temperature which is not true for the Margaree. I think it is apt to vary with the physical conditions.

Distribution of Spawned Salmon or Kelts

Dr. Belding. The Dominion Government has been tagging kelts for many years. Their movements should be considered separately from those of the maiden salmon coming on the coast.

Dr. Huntsman. I do not agree that there are essential differences. Conclusions have been drawn from the kelts as to what the others are doing.

Dr. Belding. Dr. Prefontaine and I believe that the presence of kelt in the Bay of Chaleur at different seasons indicated that at least some kelt do not leave this body of water.

Dr. Huntsman. Those put out in the northwest Miramichi estuary do not seem to particularly leave that estuary even to go down to the main river. The Restigouche recaptures indicate that where they are captured later depends upon where they are liberated, whether they have a distribution distinctly seawards or farther up.

Dr. Belding. Were they recaptured in the same year or after a winter in the sea?

Dr. Huntsman. Mostly after two winters.

Factors Affecting the Movement of Salmon

Dr. Huntsman. We believe that we cannot be very sure of interpretations of salmon movements unless we get as definite information as possible of the forces affecting the movements.

I agree with Dr. Ward that it is desirable to find out the action of the environment on the fish. I am inclined to believe that we might more or less take for granted the nature of the salmon and ask what it will do. This seems desirable in order to understand the behavior of the fish in any particular environment. For fish of any particular river we should have a thorough knowledge of the local environment to which they will be exposed and of the effects of the environment upon the fish.

Mr. Menzies is familiar with facts which seem definitely to indicate what determines some of the movements of the salmon. Drift of the water does not necessarily determine what the salmon will do but where it will be.

Temperature

Temperature is a factor which operates very widely and in extremely varied fashion and I think that probably it is pretty well appreciated. I find some relation between the time of capture and the temperature of the sea. For the Margaree in the spring when large amounts of ice are brought against the coast, nearly all the fisheries are delayed—lobster, cod and the salmon fisheries—so that it seems as if it is a definite factor determining when the fish will be taken.

Mr. Menzies. It is a little difficult to ascertain the effect of temperature if the salmon can be taken every day in the year.

Dr. Huntsman. It is difficult to ascertain the critical temperature on the Margaree coast, since there is stratification of the water. In the Bay of Fundy, particularly in Minas Channel, it is comparatively easy, as the water in that channel does not differ in temperature more than a small part of a degree from top to bottom.

Mr. Menzies. In the Tay and Spey you get salmon coming in from the sea every day.

Dr. Belding. Temperatures in January off the shores of Great Britain correspond with those in the Gulf of St. Lawrence in May and June.

Mr. Menzies. They will go up the river at 34° F., possibly 33° or 34° and freely at 34° and 35° F.

Dr. Ward. That shows the difference on the two sides of the ocean. We do not get that temperature range in the rivers on the west coast; we do get temperatures that run dangerously high.

Dr. Belding. Mr. Calderwood in an article written some years ago showed that the relative temperature of the river as compared with temperature of the sea had nothing to do with the run of the salmon into the river.

Mr. Menzies. Undoubtedly so. It must be so. Every day when the water is suitable there will be fish going up.

Dr. Huntsman. It seems as if in your rivers it merely determines how active the salmon are.

Mr. Menzies. Large numbers will go in at the lower end of the scale and large numbers at 60.

Dr. Huntsman. If the temperature goes down to 30° or 31° they stop entirely. This seems to make a difference between the rivers of the Bay of Fundy and those of the Gulf of St. Lawrence. It is definitely a factor in the stopping of movement.

Mr. Menzies. When the temperature is below 40° F. they will not go beyond 15 to 20 miles above tide. Forty to 45° is a critical temperature; below 40° they will not attempt to ascend obstructions. At 42° they will pass the obstructions freely.

Dr. Huntsman. We have differences between the two branches of the Margaree River with regard to the running. The southwest is from a lake, the northeast from high land and ravines in which the snow remains late. The local experience is that in the very early part of the season the salmon will go up the southwest when the ice water is coming down the northeast and only afterwards will they go up the northeast. This occurs only in exceptional seasons.

Mr. Menzies. Fish were going up the Dee when the water was coming nearly all from snow, we found the farther we got up, the higher the temperature of the water. There was snow but sun shining on the rocks heated it up. There was wide temperature fluctuation and temperatures apparently rose farther down the river.

SEXUAL MATURITY

Dr. Huntsman. Is there special behavior of the salmon when beginning to mature sexually or when approaching maturity? Do fish entirely mature behave like those that will not spawn for a year, and do these fish behave differently in movement from spawned fish?

Mr. Menzies. The early fish go farthest. The autumn fish spawn at the bottom of the river, the early fish going farther. You get your grilse and summer spawning fish in the middle of the area and the autumn fish in the beginning. Fish coming in last utterly fail to go up. In the Tweed, the late fish go very much farther than late fish elsewhere. Plenty of early fish there.

Dr. Huntsman. In Mr. White's experiments in the Apple River near spawning time fish entered the south branch to which they did not belong. They did not do this earlier. They showed a different behavior when very near the spawning period.

Mr. Menzies. Except in the River Tweed they function in quite a standard way. If they have gone 15 or 20 miles and a lot of them rest in a pool the spring fish coming in after them will pass them and go farther. Then about the beginning of May or June, with water temperature 48° to 55°, the whole lot will go and they will stay in the one place farther upstream all summer. Then in the autumn they will move on.

Dr. Huntsman. There is the point too that the fish coming up well before spawning time keep to deep pools and apparently do not run up any of the small tributaries and then at spawning time they are nearly everywhere they can get. They seem to behave differently at spawning time.

Mr. Menzies. The early fish go into the quiet water, deep pools, and as the water temperature rises they will move out from that into stronger water. When it gets to 60° to 65° they will move out to the rapid water.

Dr. Huntsman. Similar to having a day position in the pool and moving up to rapid water in the evening?

Mr. Menzies. Our salmon do not do that.

Dr. Huntsman. It is fairly general here.

Mr. Menzies. Once the temperature is up they will be in the strongest water.

LIGHT

Dr. Huntsman. Are they more active in the evening?

Mr. Menzies. They merely become active where they are. In the summer time when the water is in condition, the salmon mi-

grate at night. There are chances of catching them at dusk, then they will start to move farther upstream. In the springtime or really cold weather they only run for an hour or two in the day time.

Dr. Huntsman. This is the behavior observed for smolts. With temperatures going up to 60° and above, the smolt entered the trap in the middle of the day as well as at night. The next day with the temperature not reaching 60° F. none entered in the middle of the day. They have their greatest activity in the evening.

Mr. Menzies. Grilse will run up shallows in very low water, but not unless you get a strong southwest wind.

Dr. Huntsman. Parr will stay in deepish water during the day, but after sunset they will be in the shallows with fins out of water.

Mr. Menzies. Strong southwesterly wind is almost as good as night, when grilse coming up with the tide and really fighting to get over a shallow.

Dr. Rich. Have you noticed any difference in the activity when the fish are just coming out of brackish water as compared with the movements after they are well up into fresh water?

Mr. Menzies. No.

Dr. Rich. There is a distinct difference in the streams on the west coast with regard to the migration of red salmon coming up from brackish water. They start to run early in the morning at a place where we had a weir and were counting them, and in the evening they stopped in a matter of five minutes when the sun got down behind a certain hill.

TURBULENT CURRENTS

Dr. Huntsman. This subject will not be at all clear without a great deal more work. Its importance is, I believe, very great. You get such results as, if a salmon is moving about and comes into a current with turbulence it orients itself and is liable to remain; without such it becomes active, even to the extent of jumping out of the water.

Mr. Menzies. What happens when there is no turbulent current?

Dr. Huntsman. It shows no orientation at all. It may be moving about, going to and fro. It seems to be restless when away from such turbulent current.

RANDOM MOVEMENT VS. DIRECTED MOVEMENT

Mr. Menzies. Our marking experience does not suggest that the movement is quite at random.

Dr. Huntsman. The movement may be directed or it may be at random. I cannot see direction in it. It is desirable to have the facts on which is based the view that it is directed. If it is a to and fro movement, I would not call it directed.

Mr. Menzies. There surely must be direction. Of fish marked close to the mouth of the river, some are 36 days later caught at the same place, while another on the following day is caught three miles away. Otherwise it would be just chance movement.

Dr. Huntsman. It might be of interest to refer to a paper by Thompson on tagging data for the carp in the Illinois River. The only direction which he got for the carp was that there was a greater tendency to go downstream. He found the spread of the carp through the water to correspond with the formula of Einstein for Brownian movement of inorganic particles.

Dr. Belding. Several tagged fish were recaptured after 28 to 36 days, in the Miramichi drift-net fishing area. The salmon evidently move around in this area, their movements being governed in part by the local currents and weather conditions. While they probably did not leave this area they actually travelled a considerable distance in their random movements.

Dr. Huntsman. On the Margaree coast, on the basis of the results of recaptures of tagged fish, it seemed that in about two weeks those that were tagged just outside the river were uniformly distributed among the stock of salmon that occupied that area.

Mr. Menzies. Surely that was directed; the river must exercise some control over their movements.

Dr. Huntsman. River influence restricted them; as soon as they got to the edge of that influence their extension tended to stop.

Within certain limitations there is random movement.

Dr. Ward. May I point out that you have to consider in Thompson's paper that he entirely overlooked the fact that carp has no opportunity for movement according to Einstein's formula; they move within fixed sides of a narrow stream and not as in a field of equal movement in all directions. While the movement of the fish in the drift area might correspond very much more nearly with Einstein's formula, the movement of carp in a stream would meet limits.

Dr. Huntsman. We tried to apply the formula to salmon and came to the conclusion that we could not expect it to apply after a short time owing to space limitations and the effect of river influence.

Dr. Belding. Did Dr. Thompson eliminate the question of food? Naturally the movements of carp will be governed by the distribution of food in the river.

Dr. Huntsman. If the food is sufficiently uniformly distributed the random effect will not be obscured.

ODORS

Dr. Huntsman. From the facts we have it is clear that the salmon show a definite relation to their own rivers. Perhaps the best speculation is that this is determined by smell, and yet it seems as if nothing has been done in this direction to determine whether a fish can recognize the very many odors that may exist in river water as distinguished from sea water. In Mr. White's experiment with the east branch of the Apple River originally there were no young salmon that he could find, and no local salmon went up in the fall, although they went up the other branch. But, when he planted the Restigouche fry in that river, at once that fall the local salmon went up and spawned. It seems that the presence of young salmon in the river determined whether the local adults would or would not ascend the river. It would be through some odorous substance that came from the young.

I raise the point that we need to have some experiments or further observations made.

Mr. Menzies. There is no doubt at all from the observations made that there were no salmon in that river before his work?

Dr. Huntsman. It is impossible to prove a negative, but none were found.

Mr. Menzies. He actually did find a number of native smolts in the river. You would still have the lure of the salmon scent.

Dr. Huntsman. Smolts undoubtedly go up as well as down; also they go up above tidal water. Therefore, there is no more evidence that the native smolts found later came from one rather than the other river.

This result of a preference being shown for the branch with young salmon is quite in accord with his experiments with the marked fish. With both river waters there, the fish ascended the one in which they had been reared.

Mr. Menzies. It is in keeping with the salmon going back to their own river.

Dr. Huntsman. In the matter of going back to their own river, the unproved behavior is that when they are away from the river influence. Of that I am still in great doubt.

Mr. Menzies. The home to a tributary or the home to a river.

Dr. Huntsman. Since the two branches have separate estuaries that empty into a common estuary, it will be necessary to define a tributary as including an estuary, if these are not to be considered different rivers.

Mr. Cowie. The doubt exists when the salmon are 20 to 30 miles away from the mouth of the river. It would have to be the influence of the river as a whole they would have away out at sea.

Dr. Huntsman. I have believed that they might get back if random movements could bring them under the influence of their own stream.

Mr. Cowie. Take the Pacific salmon, there is a distinct difference in size between the Rivers Inlet fish and the Fraser River fish, the sockeye. There is even a slight difference between Smith's Inlet and Rivers Inlet, with a comparatively narrow peninsula between the two. Yet each kind goes back to the source from which it came.

Dr. Huntsman. You might have the combined influence acting outside and then the separate influence, each affecting its own fish.

Mr. Cowie. Salmon coming in from the sea towards the rivers must have something attracting them to certain rivers. For instance we know that two years ago a large number of sockeye going to the Fraser came round the north end of Vancouver Island. Why did they not go to Rivers Inlet which was not far away instead of going through the Narrows between Vancouver Island and the mainland to the Fraser River? There could be no mistake owing to the size of the fish.

Dr. Rich. I think I know the assumption that has been made. It was that the fish that came round the north end of Vancouver Island were presumably headed for a certain tributary or a set of tributaries of the Fraser and that they always came round there.

Dr. Huntsman. It is necessary to get sufficient facts to show that the bulk of the fish from a river get well away from river influence and go back. There is no scientific proof that that is the case.

Dr. Rich. If you can prove, and I think it is possible for you to do so, that fish go back to the home stream, then you must take that fact into consideration.

Dr. Huntsman. We need to mark the fish in the river and then trace their movements.

Dr. Powers. I have heard it said that purse-seiners fish more on the east side of San Juan Islands when the wind prevails from the west, and when the wind prevails from the east the purse-seiners fish on the west side of the islands. With westerly winds the Fraser River water is blown more around the south end of the islands, and with easterly winds the Fraser River water is blown around the north end of the islands. During easterly winds I have observed muddy Fraser River water just off Friday Harbor, and when the water was tested it was found to be less brackish.

Conservation

Dr. Belding. At the present time there is no statistical proof of a general decrease in the salmon catch because of cyclic and other fluctuations and because of marked local variations. On the whole statistics do not indicate a very great decline.

The question naturally arises as to whether increased efficiency in methods of catching is masking a real decline. Statistics should be based on the methods of catching, number of nets, boats operated, etc. We must have more detailed records for Quebec, New Brunswick and Nova Scotia before we can determine the nature and extent of a decline. On the other hand, there is evidence of a decline in certain rivers and sections, particularly in the upper tributaries of the St. Lawrence River. Therefore, we must consider that there has been a decrease, but it is evidently a decrease that can not be measured in terms of general statistics. Certain rivers have shown a decrease, but others have not.

As long as the requisite number of salmon spawn in the rivers, the supply will be maintained. When the number falls below that point a decline will set in. As far as the Miramichi drift-net fishery is concerned, it certainly has a marked local effect upon the salmon stock of the Miramichi River and a less extensive effect upon that of the Bay of Chaleur.

Tagging experiments indicate that the region near Port-aux-Basques is a crucial point for the salmon of the Gulf of St. Lawrence. There is potential danger if the drift-net fishery at Port-aux-Basques should increase to an appreciable extent. The use of boats equipped with freezers provides ample means for increasing this fishery. Any marked increase in the Port-aux-Basques drift-net fishery will affect adversely the salmon fisheries of Quebec and New Brunswick. The problem is to determine if the commercial fishery is reducing the number of salmon below the minimum necessary for the perpetuation of the salmon stock.

On the other hand the conservation of the salmon in the river by protecting the spawning salmon, by increasing the available spawning grounds and by protecting the small parr so as to yield a greater pro-

portion of smolt is an equally important means of perpetuating and maintaining the salmon supply.

Dr. Huntsman. I heartily agree with Dr. Belding as to the desirability of conservation of each generation and of stocking particular rivers to have more salmon available for all fishermen. I have the same doubts as Dr. Belding whether there is any evidence of a general drop which would have any particular effect upon the stock. Undoubtedly we have cases where the local stock in a particular river has been utterly wiped out, as in Ontario and parts of New England. There is no question at all there. But as regards those parts of the coast where fishing for salmon has gone on for a great many years there is nothing to indicate that the stock has really declined. Conservation then is particularly important with regard to the young in the river, but the other should not be disregarded.

I have seen evidence of particular tributaries which seemed to be quite suitable for adult salmon, but I felt there was a definite indication that the salmon were kept from going up those branches, any going up were removed. That would be a direction in which conservation measures for the continuing stock would be important. If such practice of destroying the fish were stopped there would be chances of increasing the stock automatically. Removal of obstructions, such as dams, might be expected to bring back the condition which existed previously.

There is the matter of conservation of the stock in the sea, whether that be with a view to getting a larger number to spawn or in order to have the catch better distributed, a better proportion going to the river for the anglers. Results of this year's tagging of salmon in the St. John outflow are not complete, but quite striking. We tagged the fish at three different points, in St. John Harbor, off Dipper Harbor, off Lorneville. We have been astonished at the very large number of recaptures from those tagged in the harbor. Unfortunately, owing to the fact that they are taken first at the inner end we have not comparable figures for all times. From June 1 to 11 the tagging was going on at all three places and the results are, therefore, comparable. I include all recaptures reported up to June 24. For the harbor there were 29 recaptures, making 48 per cent.; for Lorneville, 19, making 37 per cent., and for Dipper Harbor 2, making 20 per cent. We can not say very much as yet, but the order seen is that the farther in you get the greater the expectation of recapture, the more intensive the fishery.

Dr. Belding. Were the salmon which were tagged in the harbor caught inside or outside the harbor?

Dr. Huntsman. Those tagged in the harbor were 8 per cent caught above tidal water, 3 per cent. in the estuary, 30 per cent in the harbor and 7 per cent outside. For Lorneville, 4 per cent recaptured above tidal water, 4 per cent in the estuary, 10 per cent in the harbor and 21 per cent outside. The indications are that the fishing is more intensive inside and decreases going out to the limit of the zone of fishing.

So it does seem that, if conservation measures are required, more attention needs to be paid to the fishery inside the harbor. The weirs catch them and there are about 80 of the drift-nets, which are not large compared with those outside, but fill up the harbor at times. Some of them take quite a number of salmon.

Mr. Rodd. We buy them from the weirs for fish cultural purposes. No trouble getting 1,200 selected fish from this source.

Dr. Belding. There is a marked concentration of recaptures both in the fish tagged at Lorneville and in the harbor, a much higher percentage than that obtained from tagging operations in the Gulf of St. Lawrence.

Dr. Huntsman. On the Miramichi coast the salmon spread much more. None at all of the St. John fish were recaptured outside the zone of river influence.

Mr. Menzies. I suppose there is commercially room for more fishing at Port-aux-Basques; by that I mean that the number of nets fishing now are not catching all the available fish.

Dr. Belding. Any material increase in the number of boats on the present grounds

would reduce the catch per boat. The present area extends from a point directly south of Port-aux-Basques towards Cape Ray. Certainly you could not double the number of fishing boats on this area without diminishing the catch per boat. However, no one knows how extensive an area is available for fishing.

Nature has imposed certain limitations. The fishing is early, starting around the first of May. The ice sometimes does not go out until the last week in April. Also, the weather conditions are such that it is impossible to fish every night and severe weather necessitates the use of a short "fleet" of drift-nets. The expansion of the Port-aux-Basques drift-net fishery depends upon whether there is sufficient available territory and whether the weather conditions are favorable over a period of years.

The fishery started about 1931, only three or four boats being engaged for the first four years. The number jumped to 17 in 1935. As a result of the extremely profitable season the number of boats increased to 32 in 1936. The 1936 season proved disastrous, most boats hardly making enough to pay expenses, and as a result there were only 24 boats that fished the whole season in 1937.

Mr. Menzies. It is no worse to catch a salmon spawning than in the sea.

Dr. Belding. Probably there is greater damage in taking the spawning salmon because it has already run the gauntlet of the commercial fisheries and the anglers.

Mr. Menzies. The only difference is in the salmon's expectation of life, whether he is killed on the spawning ground or at Port-aux-Basques.

Summary

The salmon of a given species may in a locality, *e.g.*, a river, constitute a more or less distinct entity, for which the name "stock" is to be preferred. It is not known whether the differences between such local stocks are ever heritable.

Salmon from a given local stock are in some instances at least to be found in the sea long distances (hundreds of miles) from their river. It is not known whether this is a regular behavior and associated with feeding, nor is it known what proportion of the stock has this behavior.

Salmon, when in the sea, exhibit rather marked differences in the distances they travel after liberation. These differences are seen as associated with relation to rivers, but whether correlated with distance from natal river or with degree of river influence is uncertain.

Salmon return predominantly to their rivers of origin, but it is not known what proportions return, nor what conditions determine return.

Movement of salmon through a river estuary and up a river is influenced by the relative quantity of water flowing downstream, but the way in which this acts is not known.

Salmon (Atlantic) that have spawned behave differently, at least in some places, from those that have not.

Temperature is an important factor affecting the movements of salmon, but the details of its effects may differ from place to place and need elucidation.

There are indications of the behavior of salmon changing with the development of sexual maturity, but more knowledge is needed.

The behavior of salmon depends to quite an extent upon changing light conditions, but the effects of light are complex and require clarification.

It is not known to what extent the movements of the salmon are at random, to what extent they are directed, nor how they are directed.

There is as yet no knowledge of the sense of smell determining the salmon's movements.

Proof of any general decrease in the stock of Atlantic salmon is lacking. It is important (1) to have sufficient numbers of spawning salmon in the rivers to maintain the local stocks, and (2) to assure the best conditions in the rivers for the eggs and young.